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THERMOREGULATION

OF THE RED-BREASTED NUTHATCH (*Sitta canadensis*)

by

John N. Mugaas

B.A. University of Montana, 1965

Presented in partial fulfillment of the requirements for the degree of Master of Arts in Zoology

UNIVERSITY OF MONTANA

1967

Approved by:

Chairman, Board of Examiners

Dean, Graduate School

MAY 2[illegible] 1967

Date

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INTRODUCTION

I. Traditional and Contemporary Views of Homeothermy and Thermoregulation.

A. Homeothermy and Body Temperature.

1. Birds as Homeotherms.

Birds as a taxonomic group are homeothermic and keep nearly constant body temperatures over a wide range of ambient temperatures. At high ambient temperatures they can tolerate a small rise in body temperature but they must all work to prevent their body temperature from rising to a lethal level. At low ambient temperatures, however, not all birds work to prevent their body temperatures from falling to within a degree or two of the ambient temperature. Pearson (1960) classified homeotherms and their responses to low temperatures into; (1) the Obligate Homeotherms which resist lowering their body temperature as long as they possess energy reserves, for to drop their body temperature results in death, (2) the Stubborn Homeotherms which resist lowering their body temperature when their energy reserves are high, but succumb in the face of environmental stress when their reserves are depleted and drop their body temperature to near the ambient temperature, then raise it back to normal when environmental conditions once again become favorable, and (3) the Indifferent Homeotherms whose body temperatures drop to within a degree or two of the ambient temperature when they sleep, but raise spontaneously to normal when they awaken.

Birds for the most part are obligate homeotherms (Pearson, 1960). Homeothermy for them, however, is expensive, since gram for gram, among homeotherms, birds require more fuel than mammals, for they have the highest total heat production of any animal species (Benedict, 1938;

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Brody, 1945; King and Farner, 1961; Lasiewski and Dawson, 1967). In recent years, species from the Apodidae, Caprimulgidae, Trochilidae, and Hirundinidae, have demonstrated the ability to become torpid (Bartholomew et al. 1957; French and Hodges, 1959; Howell, 1961; Huxley et al. 1939; Jaeger, 1948; Lasiewski and Thompson, 1966; Marshall, 1955; Shellabarger et al. 1961; Stebbins, 1957; Thorburg, 1953). These species, like the mammalian hibernators, fall into groups two and three of Pearson's (1960) classification. McAtee (1947) gave a review of the older records of avian torpidity.

2. The body-temperature body-weight relationship of birds.

The deep body-temperatures of birds, like those of mammals are dependent on the metabolic rate and effectiveness of the body insulation. The resting body-temperature of birds, unlike that of mammals, however, is related to body-weight, and a curvilinear rise in resting body-temperature is evident with decreasing body-weight for birds weighing down to 20 g (McNab, 1966). For birds weighing less than 20 g, the curvilinear function fails, and the body-temperature begins to decrease with a decrease in body-weight. Figure 1 demonstrates the body-weight body-temperature relationship of birds and mammals. McNab (1966) combined the King-Farmer (1961) equation for predicting the metabolic rate of birds, with the Morrison and Ryser (1951) equation for predicting the conductance value of an animal's insulation and derived a formula which produced a line representing the trend of body-temperature to body-weight in birds (Figure 1). This line, though derived from relationships of metabolic rate and conductance, follows the trend of points plotted from empirically found body-temperatures of birds ranging in weight from 30 to 100,000g. The variable resting metabolic rate and the heat conductance of the insulation

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permit several conclusions to be made about not only the differences in body temperatures between birds of different weights, but also the differences in body temperatures between birds and mammals of comparable size.

Birds have a higher total heat production than mammals of comparable size (Benedict, 1938; Brody and Proctor, 1932; King and Farner, 1961; Lasiewski and Dawson, 1967), and this coupled with an effective insulation gives birds a higher body temperature. McNab (1966) stated that Lasiewski et al. (1964) presented data which demonstrated that birds of 20 to 200 g had heat conductance values for their insulation of 70% less than mammals of the same weight. Irving (1960) pointed out that the ptarmigan, which is thought to be the smallest bird suited to arctic cold by its insulation is 1/10 the size of the arctic fox, which is the smallest mammal suited to arctic cold by insulation. These relationships indicate that birds of 20 to 200 g have a lower rate of heat loss than mammals of comparable size and this along with their higher metabolic rate gives them a higher body temperature. Birds and mammals weighing 2 Kg and more have similar rates of heat loss, but the higher metabolic rates of the birds account for their higher body temperature (McNab, 1966).

The insulation of birds weighing less than 20 g is similar in value to the insulation of mammals of comparable size (McNab, 1966). The amount of surface area in comparison to body weight present in the very small animals of both homeothermic classes, limits the amount of insulation the animal can possess and still be able to move (Irving, 1960; Scholander et al., 1950a). These small birds possess, however, a higher metabolic

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Figure 1--The relation of body temperature to weight in birds and mammals.

Line A, B represents McNab's (1966) curve for predicting the relationship of body temperature to weight in birds. Portion A represents that portion fitting the empirical data. Portion B represents that portion not fitting the empirical data. Line C represents the empirical data which fails to follow the predicted values. The horizontal line D represents the mammalian standard.

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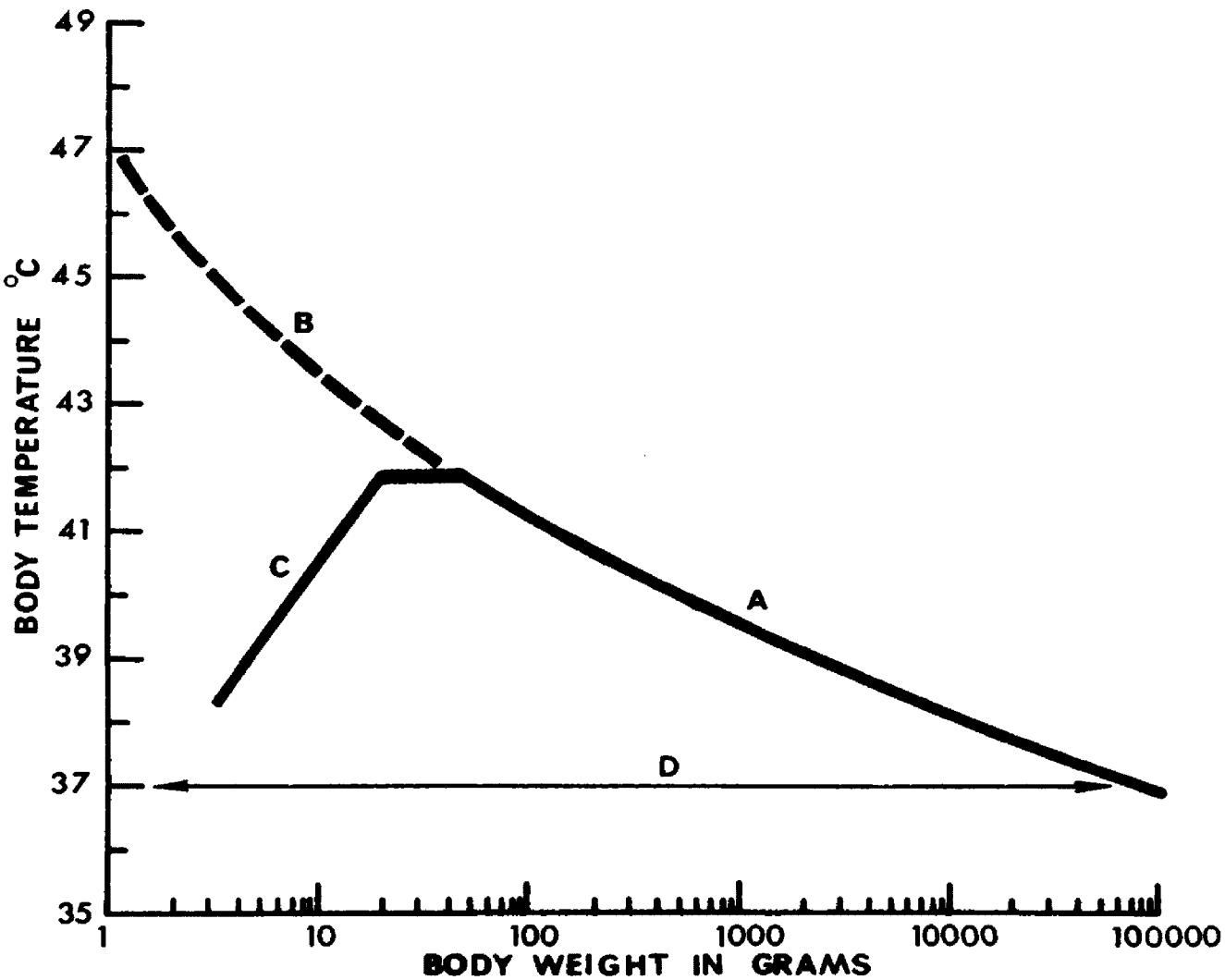

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rate than comparable sized mammals which gives them higher body temperatures (McNab 1966).

Though the metabolic rates of birds below 20 g are higher than those of mammals of comparable size, they are lower than the rates predicted from the King-Farner (1961) equation used by McNab (1966) in deriving the equation of the slope of the line representing the body temperature of birds. The lower than expected metabolism, and the higher rate of heat loss due to poorer insulation, act together to lower the body temperature of these small birds from the expected values, giving a direct rather than inverse relationship between body-weight and body-temperature.

3. Cyclic variations in the body temperatures of birds and mammals.

Wetmore (1921) studied the body temperatures of 327 species of birds from 50 families in the central United States, and described a daily fluctuation in their temperatures, the highest being recorded during midday activity, and lowest during sleep. Several authors, (Baldwin and Kendeigh, 1932; Bartholomew and Cade, 1957; Bartholomew and Dawson, 1958; Dawson, 1954; Dawson, 1958; Howell and Bartholomew, 1961a, 1961b, 1962; Irving, 1955, 1960; Irving and Krog, 1954, 1956; Kendeigh, 1934; Lasiewski, 1964; Morrison, 1962; Veghte, 1964) have since demonstrated a diurnal cycle in arctic-to-tropical birds. Fluctuations in body temperature in response to high and low ambient temperature have been experimentally produced in several species by several authors, and though the cycle is related to the ambient temperature it does not vary more than a few degrees, unless it is one of those species capable of torpor (Bartholomew et al., 1962; Brenner, 1965; Brush, 1965; Calder, 1964; Calder and Schmidt-

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Nielsen, 1966; Farner, 1956; Hart, 1962b; Howell and Bartholomew, 1959; King, 1964; Lasiewski and Dawson, 1964; Misch, 1960; Veghte and Herreid, 1965; West and Hart, 1966). Cylic variations in the body temperatures of small mammals in relation to ambient temperatures were found on an experimental, seasonal, and daily basis by several authors (Bartholomew and MacMillen, 1961; Bartholomew et al., 1964; Hock, 1951; Hudson, 1964, 1965; Hudson and Rummel, 1966; Irving and Krog, 1954; Krog et al., 1955; Leitner, 1966; MacMillen, 1965). Irving (1955) stated the daily fluctuation in the body temperature of birds may be as much as 6° C, and he recognizes three levels within the range of fluctuation; (1) the sleeping level, (2) the awake but resting level, and (3) the awake and active level. Wetmore (1921) recognized that taxonomically related species of birds often had similar or the same average body temperatures. Irving and Krog (1954) feel that the body temperature is a characteristic of each bird species, and have found little difference if any in the average resting body temperature of species from different latitudes, making the average body temperature a constant and not a variable or an adaptation to climate. Wetmore (1921) considered a seasonal variation in average body temperature unlikely and wrote "I am, in the light of the records available at present, unable to recognize any constant difference between body temperatures made in the same species at seasons of marked heat or cold".

B. Thermoregulation.

1. The logistics of thermoregulation.

Irving (1960) stated, "Body temperatures of homeothermic species are phylogenetically differentiated, but the differentiation shows no

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common regard for geographical range, and their temperatures are more stable than the climates of the earth, which have changed appreciably, while the temperatures of the birds that inhabit them have apparently remained fixed". One of the most apparent problems facing birds of every climate is that of maintaining their deep body temperature over that range of ambient temperatures afforded them by their environment. The search for those "adaptations" or modes of "acclimatization" that have allowed them to do this, as they spread to, and inhabited every climate on earth, has become, for the physiologist, the study of "Avian Thermoregulation".

a. The adjustment of heat gain and heat loss.

Over any range of ambient temperatures the control of the body temperature depends upon the rate of heat gain and the rate of heat loss from the body. If the heat capacity and temperature of a body are constant, the rate of heat loss will equal the rate of heat gain (Kleiber, 1961). The heat capacity of a homogeneous body is equal to the product of its specific heat times its mass, which means its heat capacity is equal to the quantity of heat in calories, that body gains or loses when its temperature is changed 1° C (Semat, 1962). The heat capacity of a heterogeneous body, such as an animal, is equal to the sum of the heat capacities of all its parts. Kleiber (1961) gives a formula for estimating the heat capacity of an animal body as:

Heat Capacity = (1.0 Cal/g °C)(Kg of H_2O) + (0.4 Cal/g °C) (Kg dry animal matter) where 1.0 Cal/g °C is the specific heat of water and 0.4 Cal/g °C is the specific heat of dry animal matter. Homeotherms possess a rate of minimal oxidative heat production, known as the basal

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thermostatically via its insulation, metabolism, muscular activity, and ability to refrigerate. This allows it to operate at nearly the same internal temperature over a wide range of ambient temperatures.

b. Seasonal and climatic thermoregulation.

The mechanisms controlling heat loss and heat gain in homeotherms can be altered, by either exposure for long periods at different temperatures in the laboratory, or by exposure in the wild to seasonal temperature changes. Edholm (1961) outlined Hart's three categories and definitions of these alterations as follows: (1) Acclimation describes alterations in an animal's reaction to a thermal condition when temperature is the only variable, (2) Acclimatization describes the alterations in an animal's reaction to a thermal condition as a result of climatic exposure (season, latitude, photoperiod, and temperature), and (3) Adaptation describes racial or species differences due to climate. The alterations produced are measurable through changes occurring in metabolic activity, effective insulation, heart rate, respiration rate, muscular activity (shivering), organ activity and weight, and body weight.

Indirect metabolic measurements are relatively easy to perform, and if controlled properly, yield information about the expenditure of energy at different temperatures, the relative effectiveness of the total insulation, the nature of the material providing the energy, and the effectiveness of the apparatus for evaporative cooling. Because of the quantity and various types of data available from metabolic measurements, the science of animal calorimetry has become a valuable and popular tool for workers in thermoregulation as a means of assessing an animal's thermal restrictions.

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2. Calorimetry of the body heat of homeotherms.

a. The historical development of indirect calorimetry.

Measuring the quantity of heat lost from the body (direct calorimetry) is difficult, but calculating the quantity of heat produced (indirect calorimetry) by measuring the respiratory exchange of CO_2 and O_2 is relatimely easy. Lavoisier and LaPlace (1790; from Kleiber, 1961) deduced the major quantity of heat produced by the body was due to the combination of the inspired O_2 with the C from the metabolites to form the CO_2 of expiration. Leibeg (1842; from Lusk, 1919) concluded the heat production of the body resulted from the combustion of proteins, carbohydrates, and fats, but erroneously assumed that oxygen caused this combustion. In 1852, Bidder and Schmidt (from Lusk, 1919) stated "almost all the nitrogen of protein and collagen is split from its combustion and carries with it enough carbon, hydrogen, and oxygen to form urea; the remaining part, containing 5/6 of the total heat value of the protein, undergoes oxidation to CO_2 and H_2O, which are eliminated in the respiration, the calorifacient function being fulfilled". This concept of protein catabolism was not considered valid, however, until Carl V. Voit (1857; from Lusk, 1919) proved its validity with an experiment in which he fed dogs a protein diet that contained a known quantity of nitrogen, and later recovered that same amount of nitrogen from their urine and faces. He experiments led to the concept of "nitrogen balance".

Pettenkoffer and Voit (1866; from Lusk, 1919) calculated the grams of protein and fat catabolised by a fasting man, by measuring the grams of nitrogen in his urine and the grams of carbon in his expired air. The heats of combustion of protein and fat as found in a bomb calorimeter

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were then applied directly to these calculated weights, to determine the total heat produced. Rubner (1885; from Lusk, 1919) found their determination in error, because they had failed to subtract the value for the heat of combustion of the urinary nitrogen (urea), from the heat of combustion of the protein. He concluded this was absolutely necessary since the urea represented the incomplete oxidation of protein in the body. In later studies Rubner confirmed that carbohydrates and fats are completely oxidized in the body and in 1894 (from DuBois, 1936) wrote that he could express organic heat production as the heat of combustion of catabolized compounds minus the heat of combustion of urinary components.

b. The respiratory quotient.

Using Avogadro's hypothesis, some early investigators compared the volume of CO_2 produced to the volume of O_2 consumed by an animal during a metabolic trial. Regnault and Reist (1849, from Lusk, 1919) fed different mammals combinations of foodstuffs, and then measured and compared the volumes of CO_2 expired to the volumes of O_2 consumed after each feeding. They found the ratio of the volumes varied not from species to species, but rather from foodstuff to foodstuff. Pflunger (1877; from Lusk, 1919) called this ratio the respiratory quotient

$$(R.Q. = CO_2/O_2)$$

Molecules of carbohydrate, fat, and protein each contain different ratios of the elements carbon, hydrogen, and oxygen in their chemical structures. In the catabolism of these molecules, catalytic enzymes are used as a substrate for their oxidation. Only carbohydrates and fats, however, are completely oxidized to CO_2 and H_2O, while protein oxidation is incomplete; a small part of the protein molecules being con-

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verted to urea rather than CO_2 and H_2O. An examination of a molecule of each foodstuff shows why different quantities of O_2 are consumed, and CO_2 produced in the catabolism of each.

(1). Carbohydrate respiratory quotient.

Glucose ($C_6H_{10}O_5$), the major molecule of carbohydrate catabolism, contains a 2.1 ratio of hydrogen and oxygen. This allows the formation of H_2O without extra-molecular O_2 during catabolism. Only the carbon requires extra molecular O_2 for CO_2 formation. For each molecule of O_2 consumed in the reaction, one molecule of CO_2 will be formed, giving carbohydrates and respiratory quotient of 1.0 (DuBois, 1936).

(2). Protein respiratory quotient.

Proteins, because they are incompletely catabolised, require complicated mathematics for calculating their respiratory quotient. Lowey (1911; from Lusk, 1919) computed the respiratory quotient for the catabolism of 100 g of meat protein. His calculations show that after the formation of the organic nitrogen compounds and the depletion of the molecular O_2, C and H both remain, but C in the greatest quantity. Extra molecular O_2 is required to complete their oxidation. Thus the ratio of CO_2 formed to O_2 consumed becomes less than 1.0. Lowey calculated an respiratory quotient of 0.801 for the catabolism of protein.

(3). Fat respiratory quotient.

Mobilization of fat for catabolism occurs when caloric expenditure exceeds caloric intake, and involves the hydrolysis of triglycerides to free fatty acids and glycerol, which are then catabolised for energy (Masoro, 1966). Tripalmitin ($C_{51}H_{98}O_6$) is a good illustration of the properties which give fats their characteristic respiratory quotients. The molecule contains very little O_2 and after its depletion during catabolism, both

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C and H remain. As in proteins, therefore, the ratio of CO_2 produced, to extramolecular O_2 consumed will be below 1.0, but because the ratio of H to C is greater in fats than in proteins, the respiratory quotients of fats are, lower than those of protein. One mole of tripalmitin requires 72.5 moles of O for its oxidation, and produces 51 moles of CO_2, which results in an respiratory quotient of 0.703 (DuBois, 1936).

3. The calculation of heat production by indirect calorimetry.

To calculate heat production directly from the respiratory exchange, the heat equivalent of the O_2 required for the combustion of each foodstuff must be known. Because the nitrogen in protein is incompletely oxidized, its contribution to total heat production is calculated from urinary nitrogen, and those volumes of CO_2 and O_2 involved in its catabolism are calculated and subtracted from the respiratory exchange. This leaves a ratio of CO_2/O_2 known as the non-protein respiratory quotient, from which the heat contributed by oxidation of fat or carbohydrate, or a combination of the two, can be calculated. From bomb calorimetric measurements of known masses of either carbohydrate or fat, the heat produced upon combustion of either food can be determined, and from the calculations of respiratory quotient, the quantity of extra molecular O_2 required for the combustion of either can be determined. By combining the results of these two measurements, the heat equivalent of the volume of O_2 involved in the combustion of either foodstuff can be calculated. Since the non-protein respiratory quotient values which fall between 0.703 and 1.0 represent combinations of fat and carbohydrate catabolism, the per cent of heat contributed by each to the total non-protein catabolism can be calculated. Lusk (1919) presented the Zuntz and Shumberg table which gives this

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information, as well as the caloric equivalent of a liter of O_2 at any non-protein respiratory quotient (DuBois, 1936).

Magnus-Levy (1901; from DuBois, 1936) determined that in a man who had fasted 12 to 14 hours, protein furnished 12 to 18% of the total calories. He made a table of caloric values for oxygen, based on this knowledge, which enabled experimentors to calculate total heat production from the total respiratory quotient, and thus avoid the collection and analysis of urine. Many investigators began employing a caloric value of 4.8 Cal/l to the osygen consumed by individuals who had fasted for about 14 hours, and who had a total respiratory quotient of approximately 0.82 (DuBois, 1936). The practice of measuring only the oxygen consumption soon developed, and a number of varied and specialized apparatuses were developed, the descriptions of which can be found in Lusk (1919), DuBois (1936), Brody (1945), and Kleiber (1961).

4. The role of the respiratory quotient in indirect calorimetric measurements.

a. Finding the caloric equivalent of oxygen for birds.

The procedures of indirect calorimetry have been applied to studies of avian metabolism, and the practice of omitting measurements of urinary nitrogen, and using the total respiratory quotient for determining the caloric value of the oxygen consumed have followed (King, 1957). Barott and Pringle (1941) experimented with chickens, and found the caloric equivalents for oxygen, as given in the Zuntz and Schumberg table applicable to their animals when they had a respiratory quotient of about 0.70. Henry et al. (1934) concluded from the basis of their experiments that indirect calorimetry is not a proper technique to use in determining the heat production of birds because the caloric equivalents for the oxygen

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consumed when the bird has a respiratory quotient below 0.71 are not available. Mellen and Hill (1955) suggested the metabolic rate of birds be given only in terms of oxygen consumption and not heat production. King (1957) stated, however, that ". . . even though the validity of estimating the heat production of birds through reference to the Zuntz and Shumberg table is not unequivocally established . . . the scant evidence available suggests the method is valid".

Many recent authors (Brush, 1965; Calder, 1964; Calder and King, 1963; Dawson, 1958; Dawson and Tordoff, 1964; Lasiewski et al., 1966; and Lasiewski and Dawson, 1967) have used a caloric value of 4.8 Cal/l for the oxygen consumed by a bird in the resting, unrestrained, post-absorptive condition, while others (Dawson, 1954, Dawson and Tordoff, 1959; Misch, 1960; Veghte, 1964) in similar experiments have used a caloric value of 4.7 Cal/l. Kleiber (1961) gave oxygen a caloric equivalent of 4.7 Cal/l in metabolism trials and makes no distinction as to whether the value applies to mammals or birds.

b. Respiratory quotient values below 0.71.

Respiratory quotient values below 0.71 are apparently real, and occur regularly in avian metabolism trials, and apparently represent a difference between the fasting metabolism of birds, and of mammals (King, 1957), though Kleiber (1961) reported the occurrence of these low respiratory quotients in mammals fed special diets. In the catabolism of protein, uric acid is the product of the imcomplete combustion in birds, and its formation from the protein molecule leaves behind quantities of carbon and hydrogen which require more extra molecular oxygen for their complete oxidation than if urea were formed as in mammals. The protein

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respiratory quotient of birds, therefore, is about 0.75 to 0.74, rather than 0.82 as in mammals (King, 1957; Kleiber, 1961). King (1957), in contrast to Mellen and Hill (1955), felt that protein catabolism in birds cannot explain avian respiratory quotient values as low as 0.65, and suggests instead, (1) incomplete oxidation of fat, and (2) interconversions among fat, protein, and carbohydrate as being possible sources of these low respiratory quotient values. Kleiber (1961), however, presented a reaction demonstrating the catabolism of Alanine in birds to uric acid, CO_2, and H_2O which gave an respiratory quotient value of 0.667. Kleiber, (1961) also suggested that low respiratory quotient values may indicate the synthesis of carbohydrate from fats, as must happen in the lactating cow. Carbohydrate synthesis from fat is also suggested by the work of Henry et al., (1934) who found that blood glucose in cocks rose as their respiratory quotients fell to values below 0.71. The caloric equivalent of the oxygen consumed by animals with respiratlry quotients of 0.70 to 0.65 is still an unsolved question.

c. Respiratory quotient values above 1.0.

Respiratory quotients above 1.0 indicate the synthesis of fat from carbohydrate (DuBois, 1936; Kleiber, 1961; Lusk, 1919). This can be well exemplified by the rapid fat deposition shown in geese and pigs that have been force fed grain. Bleibtreu (1901; from Lusk, 1919) obtained respiratory quotients as high as 1.33 in geese stuffed with grain. The elevated respiratory quotient resulted from the formation of an O_2 poor product, from an O_2 rich precursor, so the O_2 absorbed from the outside will be low in relation to the CO_2 produced. The fat formed from a quantity of glucose will have less heat content than the glucose from

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which it was formed, hence the reaction is exothermic. For every liter of CO_2 produced in the synthesis of fat, 0.8 Cal will be released. When calculating the total heat produced in a respiratory trial involving a respiratory quotient over 1.0, that quantity of CO_2 not involved in creating the respiratory quotient of 1.0, is multiplied by this factor (0.8 Cal) and the product is added to the other heat values (DuBois, 1936).

d. The value of the respiratory quotient as an index of the intermediary metabolism.

Kleiber, (1961) stated, "The respiratory quotient is inadequate as an index for the nature of the intermediary metabolism, and particularly of the precursor-product relationship". He feels, however, it is still a valuable tool in indicating the nature of the products being catabolised. Krog (1916) mentioned that the "assumption on which the deductions from respiratory quotients are usually based may not be strictly correct, because (1) substances other than carbohydrates, fats, and proteins may be catabolised, (2) synthesis may take place, (3) there may be a difference between the CO_2 produced in a given time interval and the CO_2 exhaled at that time". Irving et al., (1930) felt respiratory quotient values could be temporarily distorted by the retention or addition of CO_2 from the large reserves the animal possesses. Kleiber (1961) proposed, therefore, that radioactive tracers be used in determining product-precursor relationships rather than respiratory quotients.

e. The effects of low ambient temperatures on the respiratory quotient.

Kayser (1937a, 1937b) reported that absorptive animals in cold produced extra heat from lipid combustion exclusively, as indicated by their respiratory quotient. Chénier, (1954; from Masoro, 1966), Page (1957); Page and Chénier (1953) working with white rats furthered this notion, and Page

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(1957) concluded on the basis of respiratory quotients that in mammals fats were preferentially used for heat production upon prolonged exposure to cold. Masoro (1966) quoted other studies not using respiratory quotients as the criterion for fat catabolism, and concluded that cold-acclimated rats did not use fat preferentially for nonshivering thermeogenesis but rather all foodstuffs were used at an increased rate. Cold-acclimated rats, however, when fasted at cold temperatures, did not develop ketosis or hepatic fat infiltration because, unlike non-cold acclimated animals, their livers possessed a greater capacity to oxidize fat.

Scholander et al. (1950b) found no indication that cold modified the respiratory exchange of arctic animals, hence their respiratory quotients were unaffected by temperature. Krog et al. (1955) worked with wild brown and white laboratory rats (Rattus norvigicus) at Anchorage, Alaska, and found that cold did not affect the respiratory exchange or respiratory quotient of these animals. Irving and Hart (1957), and Hart and Irving (1959) in summer and winter studies of the harbor seal (Phoca vitulina) and winter studies of the harp seal (Phoca groenlandica) reported no alterations of respiratory quotient in these seals due to either season or temperature. Irving et al., (1955) worked with both summer and winter individuals of the arctic red fox (Vulpes vulpes alascensis), the Alaska red squirrel (Tamiasciurus hudsonicus preblei), the porcupine (Erethizon dorsatum myops), the black brant (Branta bernicla orientalis), and the northwestern crow (Corvus caurinus), and concluded that even though respiratory quotient changes occurred in the red squirrel, the porcupine, the black brant, and the northwestern crow, these were not the result of changing season or temperature. They concluded any variations which

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occured were merely distortions caused by the retention or addition of CO_2 from the large reserves the animal possesses. Brush (1964), however, found a significant difference in the respiratory quotient of the California quail (Lophortyx californicus) above and below the lower critical temperature, and Brenner (1965) working with the European starling (Sturnus vulgaris) found their mean respiratory quotient decreased when the ambient temperature decreased.

5. Thermoregulation at ambient temperatures below the body temperature.

Several reviews (Dawson and Schmidt-Nielsen, 1964; Gelineo, 1964; Hardy, 1961; Hart, 1957, 1962a, 1964; Hudson, 1962; Hudson and Bartholomew, 1964; Irving, 1960, 1964; King and Farner, 1961, 1964; Kleiber, 1964; West, 1962) treat in a comprehensive way the methods employed by homeotherms to preserve their body temperature in spite of a changing ambient temperature. From these reviews and the studies treated in them, several terms and a number of concepts have emerged, which describe the metabolic, evaporative, and insulative responses of homeotherms to both high and low temperatures.

a. The zone of thermal neutrality, the resting metabolic rate, and physical thermoregulation.

By applying various methods of indirect calorimetry, it has been possible to measure an animal's changes in heat production in relation to changes in the ambient temperature. Since the time of Lavoisier, the heat production of animals has been studied, and it has been established that each homeothermic species has, at a certain ambient temperature, or over a range of ambient temperatures, a minimal rate of heat production (the BMR or resting metabolic rate) which in health is sufficient to

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maintain the body temperature (Benedict, 1938; Brody, 1945; DuBois, 1936; Kleiber, 1961; Lusk, 1919). The range of ambient temperatures over which an animal can maintain its body temperature via its resting metabolic rate, is directly related to the effectiveness of its insulation. Adjustment of the insulation to maintain the body temperature at the resting metabolic rate is termed physical thermoregulation, and that range of ambient temperatures over which it is effective, is the zone of thermal neutrality.

b. Fur and feathers as insulation.

Insulation in animals is in the forms of fur, feathers, subcutaneous fat deposits, and vascular heat exchanges in the extremities which act to regulate the rate of total heat loss. Fur and feathers form an external substance of poor conductance between the skin surface, and the air. The total insulative quality of fur depends upon its depth, a quality which undergoes seasonal changes in response to high and low temperatures (Hammel, 1955; Hart, 1956). Irving (1960) compared the feather thickness of systematically related arctic and tropical birds, and found no difference between the two. He found, however, that the structure of the contour feathers of arctic birds allowed them to trap more air per mass of feathers, than the feather structure of the tropical birds. Mammals, by growing longer fur or shedding old fur, vary their insulation. This variation is apparent seasonally as well as climatically among mammals. Fluffing fur will not increase its insulative value, for as Hammel (1955) pointed out, increased convective losses from fluffed fur reduces the insulative value of the trapped air. Birds on the other hand, cannot grow longer feathers without interfering with their flight function (Irving, 1960) and so rely upon the structure of their feathers to produce

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effective dead air spaces for increased insulation when they are inactive (Irving, 1960; Veghte, 1964; Veghte and Herreid, 1965; West and Hart, 1966).

Heat dissipation through fur and feathers is facilitated by sleeking them to the body, or through other physiological or behavioral means (Irving, 1960). Dawson (1954) also mentions that under certain conditions, the feathers of birds may be important in preventing rapid radiative gains from the environment. Thus, an animal's fur or feathers, gives it a flexible system for regulating the flow of heat from its body.

c. The use of the extremities in controlling heat exchange.

The appendages of many birds and mammals are poorly insulated, and the tissues there often experience a range of temperature fluctuations never tolerated or experienced by deep body tissues. Claude Bernard in 1876 (from Irving and Krog, 1955) called attention to the heat conserving possibilities of veins investing arteries passing to the surface, and anatomists have studied this possibility for years. Bazett et al. (1948) Bazett et al. (1948) have demonstrated the presence of a temperature gradient running distally in the large artery and vein concomitant in the appendages of man, indicating the presence of a counter-current heat exchanger mechanism. Scholander (1955) mentioned the work of many researchers who demonstrated arterio-venous retes, which act as heat exchangers in the extremities of many animals and stated these may be interpreted as being adaptations for heat conservation. Irving and Krog (1955) studied the occurrance of a temperature gradient along the appendages of several mammals, and a glaucous-winged gull (Larus glaucescens) and found, "Cooling of the tissues within thick insulation and before they are exposed to cold indicates that the heat of arterial blood returns to the veins

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rather than escaping to the air", and the occurrence of sharp skin temperature gradients in the thickly insulated portion of an appendage ". . .is good evidence for the conservation of heat of arterial blood by means of a vascular heat exchange".

Many authors (Bartholomew et al. 1953; Chatfield et al. 1953; Howell and Bartholomew, 1961a, 1961b; Irving, 1960, 1962, 1964; Irving and Krog, 1955; Irving et al. 1962; Johansen, 1961; Kahl, 1963; Scholander, 1955; Scholander et al. 1950c; Steen and Steen, 1965a, 1965b; Thorington, 1966) have recently described the use of the extremities for heat conservation. Cooling the extremities to reduce the rate of heat loss from them can be accomplished by reducing the flow of blood to them. This is an especially important function for animals that are resting in cold air, on snow, or in ice water, for if their extremities were kept at the same temperature as their bodies, the rate of heat loss from them would overbalance their metabolic heat gain and severe hypothermia would soon result. The use of the extremities as avenues of heat loss, to prevent overheating of the animal during activity or severe insolation is another function of this vascular heat exchanger system. By increasing the blood flow to the extremities and raising their temperature above that of the air or water around them, great quantities of heat can be lost through them.

Irving et al. (1956) worked with swine, and Irving and Hart (1957) and Hart and Irving (1959) worked with harbor seals, and found in these animals, that cooling of their skin for heat conservation in response to cold, and warming of the skin for heat dissipation in response to activity or high ambient temperatures, gave these animals as effective an insulation as if they were covered with thick insulating fur. The cooling

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of the skin in these animals produces a temperature gradient through the underlying subcutaneous fat, which like the temperature gradients of the extremities is the result of vascular adjustments which act as modified heat exchangers. The ability of the skin and fat of these short haired mammals, and the tissues of the poorly insulated extremities to vary between a heterothermous and a homeothermous condition, as regulated by vascular modifications, allows these tissues to function effectively as a flexible form of insulation to aid the animal in conserving or dissipating heat (Irving and Krog, 1955; Irving, 1964).

d. Chemical thermoregulation.

The heat-retaining qualities of an animal's total insulation reaches a maximum at the low end of the zone of thermal neutrality. If the ambient temperature is lowered beyond the end of the zone of thermal neutrality, heat is lost through the insulation faster than it can be gained from the resting metabolic rate, and to maintain the body temperature heat gain must be increased by elevating metabolic heat production. Hardy (1961) expressed the efficiency of the increased heat production at low ambient temperatures as that percentage of the increased heat which is stored in the body. Expressed mathematically this states that:

$$\text{Shivering efficiency} = \frac{\text{heat storage rate}}{\text{(shivering heat production)} - \text{(nonshivering heat production)}} \times 100$$

In mammals, the first activity responsible for elevating the metabolic rate during short-term exposure to cold is shivering (Hemingway, 1963). Activity will also elevate the metabolic rate, but because of the quantity of heat lost via convection, due to movements, the percentage stored is

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less than if the animal were standing still and shivering (Hardy, 1961). After long-term exposure to cold, many mammals are able to elevate their metabolic rate without shivering, a process which has been termed non-shivering thermogensis (Hardy, 1961; Hemingway, 1963; Masoro, 1966).

Sellers et al. (1954) experimentally established the concept of nonshivering thermogensis, and since that time several others (Cottle and Carlson, 1956; Davis, 1960; Depocas et al., 1957; Hart et al., 1956) have furthered and added experimental support to the concept. The phenomenon of nonshivering thermogensis has been the subject of a great deal of research in recent years and is thought to be under the control of adrenal medullary hormones. Edholm (1961) considers the concept of nonshivering thermogensis as being one of the most important findings of heat production studies in years, even though it seems restricted to small, or poorly insulated mammals.

Hart(1962b), and Chaffee et al. (1963) were not able to induce a nonshivering thermogenic response from cold adapted birds injected with noradrenalin. Steen and Enger (1957), West (1962, 1965), have found shivering to be the major source of heat production in wild birds. Chaffee and Mayhew (1964) have lent support via biochemical methods to the theory of Steen and Enger (1957) that shivering in the pectoral muscles is the birds major method of increasing thermogenesis in response to cold.

Experiments by West (1962, 1965) indicated that the intensity of shivering in the pectoral muscles increased as the ambient temperature fell, and that the pattern of this shivering was unaffected by season,

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or length of exposure to cold. It appears, therefore, that birds probably cannot elevate their metabolic rate without shivering. West (1965) concluded that most small temperate, sub-arctic, and arctic birds must shiver when inactive at most of the ambient temperatures they encounter.

Freeman (1966) found, in agreement with Randall (1943) that the day-old chick, (Gallus domesticus), exhibits homeothermic control at moderate ambient temperatures (25° C to 26° C) with little or no evidence of shivering. Randall (1943) stated that even though shivering occured in young chicks after the first day, it was not effective in preventing the body temperature from dropping slightly, upon exposure to room temperature, until the seventh day and incapable of preventing hypothermia at ambient temperatures below 20° C until the down feathers were replaced with the adult plumage. Though Freeman (1966) postulated the presence of nonshivering thermogensis in the day-old fowl, he was unable to produce the nonshivering thermogenic response in them with either adrenalin or noradrenalin injections. Baldwin and Kendeigh (1932), Dawson and Evans, (1957, 1960), and Kendeigh (1939) found that the nestlings of altricial species are essentially poikiliothermic in their response to low ambient temperatures until the muscular and nervous mechanisms controlling heat production have developed, and that these often develop before an effective insulative plumage does. Dawson and Evans (1957, 1960), Kendeigh (1939), and Odum (1942) also found in some altricial species that muscle tremors occurred inversely in relation to fluctuating ambient temperatures at the same time their metabolic rates began showing a homeothermic response. Though no data, so far, has established the presence of nonshivering

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thermogenesis in birds, more species need to be examined before we can say it does not exist in them. The elevation of the metabolic rate via increased muscle tone, shivering, or nonshivering thermogenesis is termed chemical thermoregulation.

6. Graphical representation of thermoregulation at ambient temperatures below the body temperature.

a. The Newtonian model.

The classical method of representing the increase in metabolism due to chemical thermoregulation is to fit a linear regression to the metabolism values as they increase at a series of ambient temperatures below the zone of thermal neutrality. The regression line, if extrapolated to zero metabolism, should cross the abscissa at a value within the animal's normal range of body temperatures (Hart, 1957; Scholander et al., 1950b; Steen, 1958; West, 1962). By this method, that ambient temperature where physical thermoregualtion gives way to chemical thermoregulation is represented by a point where a horizontal line representing the zone of thermal neutrality crosses the regression line of increasing metabolism. This point, known as the lower critical temperature, represents that point at which the animals insulation has reached its maximum. Scholander et al. (1950b) proposed this method of representation and figure 2a illustrates these principles, with the metabolic rate being plotted on the ordinate and the ambient temperature being plotted on the abscissa.

The slope of the line representing the increase in metabolic rate is less steep in those animals possessing a wide zone of thermal neutrality than in those with a short zone of thermal neutrality (Kleiber, 1961). This fact enables us to evaluate the efficiency of the insulation

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between species by comparing not only the slope of the lines indicating the metabolic increase, but also the width of the zone of thermal neutrality. According to Scholander et al. 1950b), the critical temperature gradient ($\wedge$TC), is the difference between the body temperature and the ambient temperature at the lower critical temperature, and is by definition the greatest temperature gradient over which physical thermoregualtion is effective. The $\triangle$TC, therefore, is dependent on the efficiency of the total insulation, and the value of the total insulation can be calculated from the following equation:

$$I = \triangle TC/E$$

which is a modification of Newton's law of cooling where I is the total insulation, $\triangle$TC is the critical thermal gradient at the lower critical temperature, and E is the metabolic rate. The inverse of insulation is conductance and the efficiency of an animal's insulation can be determined by calculating its conductance value from the following equation:

$$C = E/\triangle TC$$

where C is the conductance, and E and $\triangle$TC are as above.

Scholander et al. (1950b) expressed conductance as the slope of the line representing the increasing metabolic rate and Lasiewski (1963) presented this idea graphically. This method does not require the determination of a lower critical temperature or a zone of thermal neutrality for its representation of insulation. In much of the literature on small birds and mammals, the effectiveness of the insulation is expessed as total insulation or conductance.

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b. Chemical and physical acclimatization:

Applying the principles of Scholander's Newtonian model, Hart (1957) graphed the classical picture of physical and chemical regulation and the changes which acclimatization can cause in either to provide an animal a means of surviving prolonged exposure to cold (Figure, 2b). By increasing the insulation the lower critical temperature is lowered, the zone of thermal neutrality extended, and the slope of the regression line representing chemical thermoregulation lessened to allow the lower limit of survival to be extended several degrees lower without changing the animals metabolic capabilities. If the insulation remains constant, the extention of the lower limit of survival can occur only through an extention of metabolic abilities, which means extending the original line of metabolic increase to even greater rates to cover the heat lost at the lower temperatures. This model, like Scholander et al.'s (1950b), uses a single ambient temperature as the lower critical temperature.

c. West's model of acclimatization for small birds.

In their work with small birds, Dawson (1958), Dawson and Tordoff (1959), and King and Farner (1961), suggested that the lower critical temperature was not a single well-defined point for these animals as defined by the Newtonian model, but rather that an increase in chemical regulation would preclude the attainment of maximum physical regulation, and a gradual rather than abrupt increase in metabolism would occur. Dawson (1958) mentioned also that a gradual rather than an abrupt change in metabolism occured in some of the examples used by Scholander et al.

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(1950b) in their proposal of the Newtonian model, and suggested that in some species of small homeotherms the lower critical temperature is an abstraction, though still useful from a theoretical stand-point. From the data of several workers, West (1962) calculated the insulation index:

$$I = \triangle TC/E$$

for several small birds over a range of several degrees ambient temperature. He found their total insulation increased for several degrees below the supposed zone of thermal neutrality reaching a maximum in a curvilinear fashion. He also agreed with the above workers that the increase in metabolic rate was gradual rather than abrupt in small birds, and suggested that no real zone of thermal meutrality or lower critical temperature could be described for these small animals. From these observations, West (1962) constructed a graphic model (see Figure 2c) which demonstrated the gradual increase of both the total insulation and metabolism. Where metabolism alone functioned, the slope of the curve at the lower ambient temperatures extrapolated to the body temperature as in the Newtonian model. At higher timperatures where insulative and metabolic mechanisms work together the slope extrapolated beyond the body temperature. He concluded that a definite lower critical temperature and prolonged zone of thermal neutrality probably do not exist for small wild birds. Several studies of several other species of small birds have agreed closely with West's model (Dawson and Tordoff, 1964; Hart, 1962b; Lasiewski and Dawson, 1964; King, 1964; Lasiewski et al., 1964; Veghte, 1964; Veghte and Herreid, 1965; West, 1965; West and Hart, 1966). The California quail (Lophortyx californicus), a bird considerably larger than those fitting West's (1962) model did conform to the biological application of Newton's Law of Cooling

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Figure 2-Models of metabolic and insulative thermoregulation.

(a) The Newtonian model of metabolic and insulative thermoregulation illustrating graphically the zone of thermal neutrality (ZTN) where physical thermoregulation occurs; the lower critical temperature (LCT) where the insulation reaches its maximum and physical regulation gives way to chemical regulation; and the upper critical temperature (UCT)where the animal begins to actively cool via evaporative water loss. Heat production (HP) is plotted on the ordinate, and ambient temperature(Ta^{o}C) is plotted on the abscissa.

(b) Hart's (1957) model of metabolic vs. insulative acclimatization. Line A, B represents the zone of thermal neutrality, and line A, B, B^1 is the extention of the zone of thermal neutrality as the result of insulative acclimatization. Line B, C represents the increase in metabolism above the lower critical temperature at point B. Line C, D represents the increased metabolic capability for an animal which has undergone metabolic acclimatization. This increased metabolic ability has moved the lower lethal temperature from L_1 to L_2. Line B^1, C^1, D^1 represents the decreased metabolic slope required to extend the lower lethal temperature from L_1 to L_2 when insulative rather than metabolic acclimatization occurs. Heat production (HP) is plotted on the ordinate, and ambient temperature (Ta^{o}C) is plotted on the abscissa.

(c) West's (1962) model of metabolic and insulative thermoregulation. In this model no zones of thermal neutrality, upper critical temperature, or lower critical temperature are evident and the metabolic rate (solid line) has a curvilinear relationship. In this scheme the insulation (heavy dashed line) increases slowly over a wide range of ambient temperatures. The slope of the line representing an increase in metabolism within the influence of the increasing insulation, does not extrapolate to zero metabolism at a point within the range of normal body temperatures but rather to an unpredicted point above the body temperature. That portion of the line representing chemical regulation alone (light dashed line), however, does extrapolate to the body temperature as prescribed by the Newtonian Model. Heat production in % (HP%) is on the left ordinate, insulative increase in % (In%) is on the right ordinate and, the ambient temperature (Ta^{o}C) is on the abscissa.

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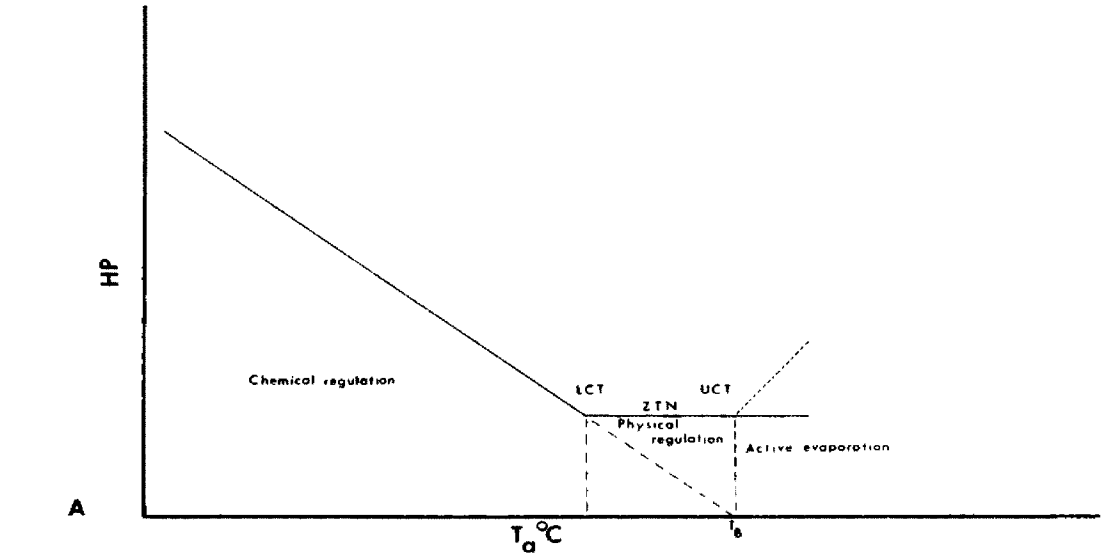

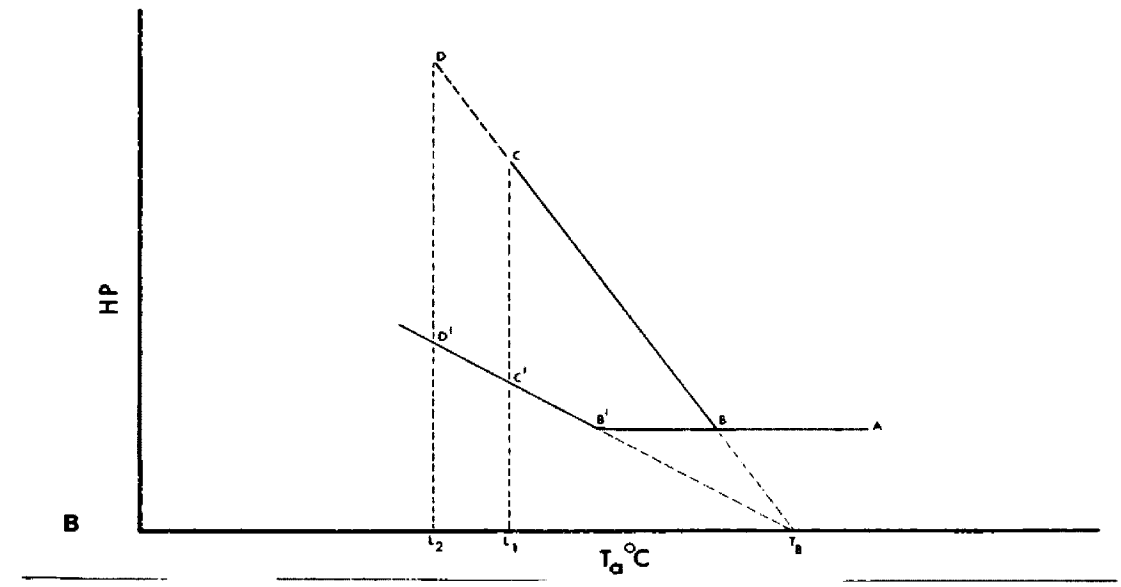

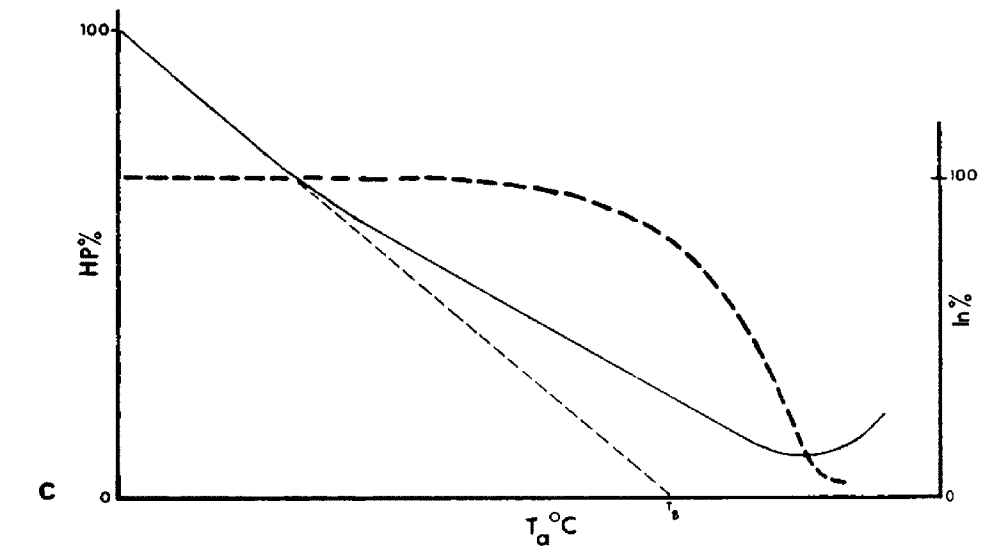

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and showed a distinct zone of thermal neutrality and lower critical temperature (Brush, 1965).

d. The validity of Newton's Law of Cooling as applied to homeotherms.

The chemical and insulative regulation models of Hart (1957) and West (1962) predicted that the slope of the line representing chemical regulation alone would extrapolate to the body temperature in agreement with Newton's Law of Cooling. It is interesting to note, however, that a great deal of variability on this point has occured throughout the literature on small birds and mammals. Various investigators working with birds (Barott and Pringle, 1946; Cade et al. 1965; Dawson, 1954, 1958; Hart, 1962b; Kendeigh, 1944; Misch, 1960; Salt, 1952; Steen, 1958; Wallgren, 1954), and others working with mammals (Bartholomew and MacMillen, 1961; Bartholomew et al. 1964; Hart and Irving, 1959; Irving et al. 1956; Irving and Hart, 1957), found that the slope of the line representing chemical regulation did not extrapolate back to the abscissa at a value within the normal range of body temperature but rather to an unpredicted value. King (1964) believed it fortuitous that his regression line for the metabolic increase in white-crowned sparrows (Zonotrichia leucophrys gambelii) extrapolated to body temperature and suggested it may not have done so had the birds been examined at a wider range of ambient temperatures. Data from other investigations of birds (Brush, 1965; Calder, 1964; Dawson and Tordoff, 1959, and 1964; Lasiewski, 1963; Lasiewski et al. 1964; Lasiewski and Dawson, 1964), birds and mammals, (Scholander et al. 1950b; and Irving et al. 1955), and mammals, (Bartholomew et al., 1964; Hudson, 1964; Irving et al. 1956; Krog et al. 1955; Leitner, 1966; MacMillen, 1965), however, fit the Newtonian model fairly well with the slope of the line

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representing chemical thermoregulation extrapolating back to within the range of normal body temperatures. Kleiber (1961) felt the Newtonian model of heat loss could not really apply to homeotherms, because Newton's Law refered to the loss of temperature, not to a loss of heat. Kleiber (1961) stated, "It is therefore unlikely that Newton's Law of Cooling is properly applicable to the heat loss of homeotherms where there is no decrease in temperature and therefore no cooling. The influence of body size on the rate of temperature loss (cooling) is different from the influence of body size on the rate of heat loss (without cooling). The application of Newton's Law to the heat loss of homeotherms would imply there is no such difference". King (1964) was in general agreement with Kleiber's opinion.

e. Thermal conductance and total insulation of small birds and mammals.

Using the principle that a lower critical temperature can be estimated, and expressing maximal insulation in terms of conductance, Lasiewski (1963) and Lasiewski et al. (1964) computed a graph which showed that for small birds and mammals conductance increased inversely with decreasing body weight. Their graph showed that the conductance values for birds of both temperate and arctic areas are lower than those for mammals of comparable size from the same area. This indicated that the feathers of these smaller birds were better insulators than the fur of the small mammals, which agreed with the concepts of Veghte and Herreid (1965) for birds and Hammel (1955) for mammals. Misch (1960), using the Newtonian model, calculated the total insulation of several birds from the literature as well as the northern blue jay (Cyanocitta cristata bromia) and from her study found she could relate, in most cases, the

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effectiveness of the insulation with the birds yearly thermal cycle. King (1964), cautioned against using insulation and conductance values calculated from an estimated lower critical temperature for indicating more than physiological differences between animals because of the errors involved in identifying the lower critical temperature.

7. Thermoregulation at ambient temperatures above and equal to the body temperature.

a. Hypothermia vs. hyperthermia.

Baldwin and Kendeigh (1932) demonstrated that the upper lethal body temperature was the same for embryonic, neonatal, juvenile, and adult birds, but that the lower lethal body temperature varied with age, being highest in adults; even so many adult birds, as well as neonatal and juvenile birds, withstood lowering their body temperatures by 10° C while no age group withstood a rise in body temperature of more than 4°C. This demonstrates not only the poikiliothermic nature of immature birds, but also indicates the narrow margin which exists between the normal and upper lethal body temperature in adult and immature homeotherms. Destruction of metabolic enzymes and other proteins within the cells occur at the upper lethal body temperature and hence heat death results from irreversable cellular destruction. Once an animal's body temperature begins to rise, the rate of its metabolic heat gain reactions increases logarithmatically in accordance with the van't Hoff effect (Q_{10}), which elevates the body temperature even more. If heat gain were allowed to continue uncontrolled, the metabolic rate would continue to increase until denaturation of the enzymes at the lethal body temperature caused

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the metabolic rate to fall off and stop (Brody, 1945).

Hypothermia without freezing, has a wider range of safety and does not destroy cells. Rapid rewarming of an animal whose body temperature has been lowered several degrees will often restore it to normal with no ill effects (Burton and Edholm, 1955). Kreyberg (1949) considered that low body temperatures, whether accompanied by freezing or not, probably do some tissue damage though he does not consider the damage irreversable and lethal as in heat coagulation. Death from hypothermia in homeotherms probably results from circulatory failure and changes in the nervous tissue from anoxia. Indifferent and stubborn homeotherms, can lower their body temperatures to levels that would be fatal to obligate homeotherms, although many of the former also have limits below which their body temperatures cannot be safely lowered (Kleiber, 1961).

b. Regulating the body temperature at high ambient temperatures.

An animal's activity is more restricted, and his thermal boundaries more defined and limited at high environmental ambient temperatures than at low ones. Most of the reviews on thermoregulation mentioned earlier discuss problems of controlling the body temperature at high ambient temperatures, but four reviews in particular (Dawson and Schmidt-Nielson, 1964; Hudson, 1962; Hudson and Bartholomew, 1964; King and Farner, 1964) deal with the thermoregulatory problems of homeotherms living in hot environments.

(1) Passive heat loss.

As long as the ambient temperature remains below the body temperature, convection, and radiation can be used by the animal as avenues to dissipate heat, but when the ambient temperature is greater than the body temperature the animal gains heat from his environment through these

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former avenues of heat loss. Heat loss via conduction, convection and radiation is aided or restricted by vasodilation or vasoconstriction, and so can be controlled to some extent by changes in the total insulation, and hence is thermoregulatory in nature.

(2) Evaporative heat loss.

The only other known method for losing heat is by the evaporation of water from moist body surfaces. Many homeotherms sweat, thus producing on their body surface a wet area for evaporation. Some other homeotherms unable to sweat, create a wet surface for evaporation by drooling copious quantities of saliva onto their body surface, and still others, incapable of sweating or drooling, evaporate water from their respiratory surfaces.

Birds, because they lack sweat glands and do not drool, evaporate water for cooling from their respiratory surfaces by panting (Baldwin and Kendeigh, 1932; King and Farner, 1961; Salt and Zeuthen, 1960). Panting, however, requires a large expenditure of energy, which reduces its efficiency for cooling, as the metabolic rate and body temperature often became elevated as a result of the animal's efforts. Species from several orders of birds, however, supplement panting with a resonant process known as gular fluttering. By gaping their mouths and fluttering their highly vascularized, moist gular area, these species can evaporate large quantities of water with little expenditure of energy, and so maintain their body temperatures for hours at ambient temperatures as high as 47°C without increasing their metabolic rate. The mechanism of gular fluttering has been reported in pelicans and herons (Bartholomew and Dawson, 1954a), doves (Bartholomew and Dawson, 1954b, boobies (Howell and Bartholomew, 1962), caprimulgids (Cowles and Dawson, 1951; Bartholomew et al., 1962;

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Lasiewski and Dawson, 1964; Lasiewski and Bartholomew, 1966), and has been observed in cormorants, owls, and roadrunners. Evaporative cooling is a physiolcgically active process, initiated at the upper critical temperature (Figure 2a).

(3) The use of hyperthermia in aiding heat loss.

As the ambient temperature approaches the body temperature heat loss via condution, convection, and radiation becomes limited due to the decreased thermal gradient, but by storing heat and controlling its body temperature at a new and higher level, the animal restores the critical thermal gradient to a level which allows passive heat loss to be effective. If the ambient temperature continues to rise, or the animal becomes active to the point of overheating, passive heat loss must be augumented with evaporative cooling. Because air can carry more water vapor as it warms, the hyperthermic condition of the animal aids the process of evaporative cooling, making it quite effective at high temperatures. Once the body temperature has reached the upper limit of safety, active cooling becomes more important, and finally if the ambient temperature exceeds the body temperature evaporative cooling is the only means by which body heat can be lost. Hyperthermia, therefore, is important in aiding both passive and active heat loss, though it is by its very nature self-limiting (King and Farner, 1964). Though body temperature in birds is not adapted to climate (Baldwin and Kendeigh, 1932; Irving and Krog, 1954; Wetmore, 1921), they have exploited their high body temperatures and their ability to tolerate periods of hyperthermia, to aid physical and active cooling, as a preadaptation for invading both hot-dry and hot-humid climates.

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(4) The effectiveness of evaporative cooling in birds.

Several researchers, (Bartholomew and Dawson, 1953; Benedict and Lee, 1937; Brush, 1965; Dawson and Schmidt-Nielsen, 1964; Hudson and Brush, 1964; Kayser, 1930, from Lasiewski, 1964; Wallgren, 1954) using open flow metabolism apparatuses, tested the effectiveness of panting for evaporative cooling in small birds and concluded they were capable of losing only about 1/2 of their metabolic heat production via this avenue. Several other species, however, when tested in this same type of apparatus were able to lose all of their metabolic heat (Bartholomew et al. 1962; Cade et al. 1965; Calder, 1964; Calder and King, 1963; Calder and Schmidt-Nielsen, 1966; Lasiewski and Dawson, 1964; Lasiewski and Bartholomew, 1966; Lasiewski et al. 1966). Lasiewski et al. (1966) in a series of experiments on evaporative water loss in birds, found that the effectiveness of evaporative cooling in open flow systems depends to a large extent upon the relative humidity in the animal chamber, and that the relative humidity in turn depends upon the rate of flow of initially dry air into the chamber.

The extent of evaporative cooling is directly related to the difference in water vapor pressure between the air and the evaporating surface (Burton and Edholm, 1955; King and Farner, 1964; Lasiewski et al. 1966). In birds the water vapor pressure at the evaporative surfaces (mucosa of the bucal cavity, trachea, pulmonary system, and air sacs) approximates that of water at the core temperature, and is therefore quite constant. The water vapor pressure of the air, which depends upon the relative humidity and air temperature, is variable (King and Farner, 1964). Therefore, the higher the relative humidity of the outside air, the smaller the difference in water vapor pressure becomes, which restricts the loss

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of vapor from the evaporative surface. Hence, the efficiency of the evaporative cooling becomes limited. In view of these facts, Lasiewski et al. (1966) felt the upper lethal ambient temperatures of birds obtained in open flow systems should be rechecked in light of the relative humidity in the chamber. These authors also believe all birds must be able to dissipate all their metabolic heat via evaporation at high ambient temperatures if the relative humidity is low.

C. The Standard or Minimal Resting Metabolic Rate, and its Relation to the Environment.

1. The standard or minimal resting metabolism.

a. The metabolic rate, weight relationship of mammals.

Rubner, (1883, from Kleiber, 1961) deduced from his experiments with dogs and other homeotherms that a fasting homeotherm would produce daily when at rest 1,000 Kcal of heat per square meter of body surface. This idea became accepted as Rubner's Surface Area Law of the metabolic rate. Benedict (1938) doubted the validity of the Surface Area Law because of the large amount of contradictory data, and set out to find empirically a more accurate method of expressing the standard metabolism. He standardized conditions under which the metabolic rate could be considered minimal, a set of conditions closely followed even today; (1) the animal must be in a natural posture and at complete rest, (2) he must be in a post absorptive state, (3) the ambient temperature at the time of measurement must be within the animal's zone of thermal neutrality, (4) the animal should not have been acclimated prior to the tests, (5) no emotional stress should be present, (6) the animal should be in a state of

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sexual repose, (7) the nitritive condition of the animal should be good, and (8) the animal should be a prime mature adult. Meeting these conditions in his own measurements of standard metabolism, and using data from other workers who had followed these conditions, he accumulated data for animals varying in size from a mouse to an elephant. He found, when the log of the total resting heat production of an animal (Kcal/24 hrs.) is plotted against the log of the total weight (Kg) and compared to similar plots of animals of different weights and species, a linear increase in heat production occurred with increasing weight. He further examined his collected data for agreement with the Surface Area Law and concluded that metabolic heat production was not regualted by the amount of surface area abailable for heat loss, but rather that heat loss must be regulated by the amount of heat produced. Scholander (1955) discussed climatic adaptations of homeotherms and expressed this same opinion and stated "the nonadaptability of the resting rate shows that heat production is not determined by heat loss, as one might infer from the Surface Law of Rubner, but visa versa. Whatever the surface area happens to be, the heat loss from it must be so regulated by various means that it blanaces heat production. In a homeotherm one might say the body temperature plays first violin, metabolic rate the second, and heat loss the third. The surface area is but one of the several factors which determine heat loss".

Kleiber (1961) pointed out that the regression equation describing the log-log plot of the metabolism to weight relationship of Benedict's (1938) mouse to elephant curve, is very similar to a curve produced by him in 1932 for animals varying in size from a dove to a steer, and a later curve in 1947 which included data for animals ranging in size

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from a mouse to a whale. In all instances the slope of the line demonstrated an expotential relationship between standard metabolism and body weight such that:

$$\log MR = \log a + b \log W$$

where MR is the metabolic rate in Kcal/24 hr, W is the weight in Kg, and a (the y intercept) and b (the slope) are empirically derived constants. Because of the direct relationship demonstrated on the log-log plot, the equation can also be expressed as:

$$MR = a\ W^b$$

with the symbols the same as above. Kleiber (1961) concluded empirically, that the equation for mammals should read:

$$\log MR = \log 69 + 0.756 \log W$$

that is "for all practical purposes one may assume that the mean standard metabolic rate of mammals is seventy times the 3/4 power of their body weight (in Kg) per day, or about 3/4 power of their body weight (Kg) per hour".

b. The metabolic rate, weight relationship of birds.

Though the validity of Kleiber's (1961) equation is empirically sound for mammals, some question as to whether it is valid to express the metabolic rate-weight relationship for birds as a 3/4 power of their weight has arisen.

(1) The Brody and Proctor equation:

Brody and Proctor (1932, from Lasiewski and Dawson, 1967) examined the data for birds and offered the following equation to describe their relationship:

$$\log MR = \log 89 + 0.64 \log W$$

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In their equation, the resting metabolism increases with an increase in weight at a different rate than it does for mammals, and is expressed by an exponent of 0.64 rather than 0.756.

(2) The King and Farner equation.

King and Farner (1961) could not conceptualize on theoretical grounds why one homeothermic class should have a different metabolic rate-weight relationship than another. On this assumption they re-examined the recent data, as well as that of Brody and Procter, and concluded the difference lay in the fact that the large birds used by Brody and Proctor had been measured at night, while the small ones had been measured during the day. Assuming a diurnal variation in standard metabolic rate as being the factor causing the difference in the Brody-Proctor equation, they eliminated the data for small birds, and arrived at the following equation:

$$\log MR = \log 74.3 + 0.744 \log W$$

which is very close to the equation given for mammals by Kleiber. They then combined the data for all birds, large and small alike, and produced this equation:

$$\log MR = \log 80.1 + 0.659 \log W$$

which is very similar to the Brody-Proctor equation. They concluded, however, that their first equation was a more valid theoretical expression of the metabolic rate-weight relationship for birds because it agreed with the relationship for mammals. They also assumed that the collection of more data on small birds would give the line a curvilinear quality at the lower weights.

(3) The Lasiewski and Dawson equation.

Lasiewski (1963) found that the King-Farner equation for large birds came closer to expressing the metabolism of his hummingbirds than the

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Brody-Proctor equation. In the same paper he agreed with a suggestion by Dawson that the King-Farner equation for large birds may represent the metabolism of non-passerines, while the Brody-Proctor equation, because it included both passerines and nonpasserines, may come closer to representing the metabolism of passerines. Lasiewski and Dawson (1967) agreed with King and Farner's opinion that there should be no difference in the metabolic rate-weight relationship in the homeothermic classes, and re-examined all the data available for birds, on the basis that passerines as a group should show the same weight regression coefficient as nonpasserines of comparable size. In their review of avian metabolism they concluded there was no diurnal variation in resting metabolic rate among birds and so clumped data collected at night with data collected during the day for each group. Their first equation represents all the data available for passerines:

$$\log MR = \log 129 + 0.724 \log W$$

the second represents the data available for nonpasserines varying in size from hummingbirds to ostriches:

$$\log MR = \log 78.3 + 0.723 \log W$$

and their third combines all the data for both passerines and nonpasserines:

$$\log MR = \log 86.4 + 0.668 \log W$$

Their results demonstrate that the weight regression coefficient is essentially identical in both passerines and nonpasserines, but that passerines operate at a higher level of metabolism than nonpasserines of comparable size. Their equation representing all birds is very similar in both slope (b) and y intercept (a) to the Brody-Proctor equation, but they consider this an artifact of combining passerine and nonpasserine birds. They feel that the real significance of their study lies in the agreement of the b-values for

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the two groups of birds when considered separately, and that this provides support to the view that metabolism of both birds and mammals varies similarly with body weight.

2. Resting metabolism and climate.

Scholander et al. (1950b) examined the standard metabolic rates of tropical and arctic animals in an attempt to find climatic differences between them. The resting metabolic rates of the species they studied fell very close to the regression line representing the mouse to elephant curve of Benedict (1938). These authors concluded that the standard metabolic rate is not adapted to climate, a view subsequently supported by other studies on arctic and subarctic species (Irving et al. 1955; Krog et al. 1955). In 1955, Scholander wrote ". . .basal heat production has been found to be essentially the same in all climates, inasmuch as most arctic, temperate, and tropical mammals fit the mouse to elephant curve of Benedict (1938). Birds show this regularity too. This leaves heat dissipation as the only major avenue for phylogenetic adaptation to climate".

a. Adaption of the metabolic rate by hibernators.

Because the poor-will hibernates, and the pauraque (Nyctidromus albicollis) another caprimulgid, has a standard metabolic rate below the predicted value for comparably sized passerines, Scholander et al. (1950b) attributed the pauraque's low metabolic rate as an adaptation possessed by all hibernators. This concept though interesting is yet to be proven. In a later study Lawiewski and Dawson (1964) demonstrated with their data for the common nighthawk, and Scholander et al's. (1950b) data for the pauraque, that even though the standard metabolic rates of these two caprimulgids are below the predicted value for passerines, they fit the King-Farner (1961)

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equation for nonpasserines fairly well, with the pauraque being somewhat higher then predicted. Since these authors further found that only starvation induced torpor in the common nighthawk it would appear that neither the pauraque nor the common nighthawk possess any special metabolic adaptations which may be common to hibernators.

Benedict (1938) found that the marmot, a hibernator, had a standard metabolic rate far below those of other comparably sized homeotherms, and that unlike a goose of comparable size, a rapid gain in weight from fat deposition in the marmot did not increase its standard metabolic rate as it did in the goose. He concluded that the marmot's fat, unlike goose fat, must be metabolically inactive. Hudson (1962) in presenting his and Bartholomew's unpublished observations on the round-tailed ground squirrel (Citellus tereticaudus) and the pigmy opossum (Cercaertus nana), found that the fat deposits in these hibernators exerted little effect on their standard metabolism. They cautioned, therefore, that before a low standard metabolism can be used as a phenomenon characteristic of hibernators, rates for comparison with those of nonhibernators should be calculated on a fat free basis. Hudson (1962), therefore, states that hibernation may either allow or follow a low basal metabolism.

b. Adaptation of the metabolic rate for life in hot arid climates.

Hudson (1962) reported that desert animals are often faced with ambient temperatures that demand a maximal effort toward heat dissipation, and therefore, proposed that if diurnal forms in this environment had a lower standard metabolic rate, it would reduce the problem of heat dissipation. Bartholomew et al. (1962) offered as an example of this type of climatic adaptation, the poor-will (Phalaenoptilus nuttallii), a caprimulgid

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that nests in the open, exposing itself throughout the day even in the desert, to severe insolation. This bird possess a standard metabolic rate of 1/3 the predicted value, which undoubtedly contributes to the birds efficiency in cooling itself at the extremely high ambient temperatures it encounters.

Another possible adaptation of the standard metabolic rate to the environment is described in a review by Hudson and Bartholomew (1964) whereby they mentioned that an animal's entry into torpor at high ambient temperatures would be facilitated by its having a lower critical temperature above the ambient temperatures to which it is normally exposed. Morrison (1960) suggested this adaptation would be useful to diurnal homeotherms living in hot environments. Interestingly enough this adaptation has recently been found not in diurnal animals, but rather in the small nocturnal rodents living in the hot arid regions of the southwestern United States. Many of these species which estivate or show signs of daily torpor, do not possess conspicuous fat deposits, but do have unusually low metabolic rates within their zone of thermal neutrality. As a result of their lowered metabolic rate, their lower critical temperature is high, being above the ambient temperatures to which they are normally exposed. This allows these animals to enter the torpid state and lower their body temperatures at relatively high ambient temperatures (Hudson and Bartholomew, 1964). The phenomenon of torpor at high ambient temperatures and a lowered metabolic rate have been found in the kangaroo mouse, Microdipodops pallidus, (Bartholomew and MacMillen, 1961); the pigmy mouse, Baiomys taylori, (Hudson, 1965); the cactus mouse, Peromyscus eremicus, (MacMillen, 1965); the brush mouse, Peromyscus boylei, and the pinon mouse, Peromyscus truei, (MacMillen, 1965; from personal communication with Hudson, 1965); and

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the California pocket mouse, Perognathus californicus, (Tucker, 1962); all of which are nocturnal. Two other southwestern rodents capable of torpor at high ambient temperatures, but which are diurnal in habit are the mohave ground squirrel, Citellus mohavensis, (Bartholomew and Hudson, 1960), and the roundtailed ground squirrel (Hudson, 1964). Significantly the diurnal antelope ground squirrel, Ammospermophilus leucurus, neither hibernates nor estivates, and does not show a reduced resting metabolism (Hudson, 1962, from Hudson and Bartholomew, 1964). MacMillen (1965) in analyzing the advantages of a low standard metabolism, and its application to aestivation in the cactus mouse, pointed out that torpor at the relatively high ambient termperatures at which it must occur in the burrow during the summer, may operate not only as a water conserving mechanism, but also as a means of prolonging food stores.

We see, therefore, that the standard metabolism has been adapted in some cases to allow survival, especially in hot arid regions (Bartholomew et al. 1962; Hudson, 1962; Hudson and Bartholomew, 1964; MacMillan, 1965) where heat loss and water conservation are factors directly concerned with and benefited by a below normal standard metabolic rate.

II. The Present Study

The red-breasted nuthatch (Sitta canadensis) is a small bird resident in the coniferous forests of the north temperate region of North America ranging as far north as Anchorage, Alaska, in the west, and James Bay, and Newfoundland, in the east. They are found as far south as southern California, southeastern Arizona, and southcentral Colorado in the west, and eastern Tennessee, and western North Carolina in the east. Populations at high latitudes and altitudes may migrate erratically and records indicate

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these nuthatches are found occasionally during the winter as far south as southern Arizona, southern New Mexico, Texas, southern Louisiana, southern Mississippi, and northern Florida (AOU Checklist, 1957).

Their widespread distribution presents them with an extremely wide range of yearly temperatures. In the Rattlesnake area near Missoula, Montana, where I trapped several of these birds, they may encounter air temperatures in the winter as low as -36° C to -40° C (Bakus, 1959). Summer temperatures have been reported in excess of 38° C at the Missoula County Airport (Personal communication), though in the shaded forests where these birds are found, the high summer temperatures are probably much lower. Even so these birds may encounter a 70° C or more yearly change in temperature in the Missoula area.

Because of their small size (weight range from 9.8 to 14.5 g), the effectiveness of their feathers as insulation may be reduced, and the rate of heat loss from their bodies at low ambient temperatures may be relatively high. To equate heat loss with heat gain, therefore, heat production may be elevated during the colder parts of the year. In the winter months as the number of daylight hours for foraging diminish, and heat production is elevated, maintainance of the energy balance may become a problem. During the summer the problem is reversed, becoming one of dissipating enough heat to balance heat gain with heat loss. The thermoregulatory problems that this small bird faces in its environment make it a subject of interest to the physiologist.

It has been the purpose of this study, therefore, to examine the metabolic, evaporative, and insulative capabilities of the red-breasted

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nuthatch when taken from the field at different seasons and presented with a wide range of ambient temperatures under controlled laboratory conditions. Metabolic rate was measured and recorded in terms of oxygen consumption over a 73° C temperature range. The production of CO_2 was measured over this entire range of ambient temperatures during certain intervals of O_2 consumption, to determine via the resultant respiratory quotient, the nature of the food products being catabolised. To evaluate the relative effectiveness of the bird's mechanism for evaporative cooling, water loss was sometimes measured along with oxygen consumption at ambient temperatures above 0° C. The effectiveness of the insulation was determined indirectly from the record of oxygen consumption by the presence and extent of the zone of thermal neutrality.

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MATERIALS AND METHODS

I. Trapping and Maintainance.

For the experiments conducted from May, 1966, to September, 1966, and from January, 1967, through February, 1967, I captured 20 red-breasted nuthatches near Missoula, Montana. Ten were taken from January through March, 1966, six from June through August, 1966, and four from December, 1966, through February, 1967. All the winter-caught birds came either from Rattlesnake Creek, 5 miles north of Missoula, or from lower Pattie Canyon, 4 miles east of Missoula. Early in the summer, from June to the middle of July, I trapped on Rattlesnake Creek. All of these sites were at elevations between 3400 and 3500 feet (United States Department of Interior Geological Survey, 1903). Late in the summer, from the end of July to the end of August, the birds apparently moved to higher elevations and were trapped in upper Pattie Canyon, 6 miles east of Missoula, at elevations of about 5000 feet (United States Department of Interior Geological Survey, 1903).

In all cases the birds were collected in a ponderose pine (Pinus ponderosa) forest. Along the stream bottom on Rattlesnake Creek, this pine was in association with northern black cottonwood (Populus trichocarpa), whereas in Pattie Canyon ponderosa pine forests dominated south-facing slopes, but were in association with Douglas-fir (Pseudotsuga taxifolia) and western larch (Larch oxidentalis) on north-facing slopes.

During the winters, three to four chicken-wire baskets filled with suet, each tied to the trunk of a tree at about chest height were used to attract the nuthatches and to accustom them to feeding in one particular area during parts of their daily foraging cycles. Though successful in the winter, these feeders did not attract the birds during the summer.

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Other wintering birds also seem feeding at the suet baskets were the black-billed magpie (Pica pica), black-capped chickadee (Parus antricapillus), mountain chickadee (Parus gambeli), hairy woodpecker (Dendrocopos villosus), brown creeper (Certhia familiaris), downy woodpecker (Dendrocopos pubescens), Clark's nutcracker (Nucifraga columbiana), golden-crowned kinglet (Regulus strapa, and white-breasted nuthatch (Sitta carolinensis).

The red-breasted nuthatches proved difficult to capture in mist nets, but could easily be live-trapped in small (40 x 20 x 20 cm) box traps, constructed of 1/2 inch mesh hardware cloth, of the type used by McCowery (1961) to trap chickadees. These were baited with suet and/or mealworms (Tenebrio molitor) and placed on a horizontal branch within 50 feet of the feeders. Each trap was equipped with a perch which functioned as a trigger, but which proved unreliable. Consequently I released the trigger manually via a string. During those days or hours of the day when the traps were left unattended, their doors were locked open to encourage their use as regular feeding spots.

In the summer, a meal-worm baited trap, attached to a small portable decoy cage containing a captive nuthatch, was positioned either in a tree or on a stump near a tree. The decoy by his calling attracted another nuthatch, and after a period of mutual displaying, the attracted bird would be lured by the meal-worms into the trap.

After capture, the birds were banded, placed in small indoor cages and allowed to adjust to captivity. An ad libitum diet of meal-worms, raw spanish peanuts, peanut butter, and water was provided. The birds adapted rapidly, eating and drinking freely soon after capture and some individuals accepted meal-worms from the hand the same day they were captured.

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After the initial adjustment period the birds were turned into a large 6 x 6 x 9 ft outdoor flight cage, containing a wooden floor, a sloped asphalt papered roof, and sides and doors of galvanized window screen. Maintained in this manner, they were constantly exposed to the natural photoperiods and temperatures of the Missoula area. Nest boxes, logs, stumps, branches, and small conifers placed within the cage allowed the birds to perch, climb, and hide. Suet, raw spanish peanuts, a peanut butter-bacon fat mixture, water in the form of free water or snow, and 20 to 30 meal-worms per bird, per day, kept the birds vigorous and healthy, and maintained their weight between 11 and 14.5 g. Immediately after capture, summer birds and those caught in the second winter, weighed from 9.8 to 11 g, but gained 1 to 2 g in captivity.

II. Experimental Procedures:

All birds used in the experiments were kept in small cages in the laboratory with food and water provided ad libitum, for at least 12 hours before testing. They were weighed on a Mettler balance to the nearest 0.01 g, before and after each test period. At temperatures from -16° C to 39° C, test periods were 6 to 9 hours in length, and two determinations, each at a particular temperature separated by not less than 10° C or more than 20° C, were conducted for each period. At temperatures from -30° C to -17° C and from 40° C to 43° C, test periods did not exceed 2 1/2 hours in length, and yielded one determination at one particular temperature per test period. Only those low values constant over at least a 2 min period (King, 1964) were selected for calculating O_2 consumption. In many cases constant values were obtained for periods exceeding 20 min.

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Those records not meeting these minimum requirements were not used. CO_2 production was determined over the entire 73° C temperature range, but evaporative water loss was measured only at temperatures above 0° C.

Any birds showing signs of molting or unusual weight loss were not used in the experiments. In those experiments conducted from May, 1966, to September, 1966, O_2 consumption was measured in six of the 10 birds caught during the first winter, and all six of the summer caught birds. The summer caught birds also provided data of CO_2 production and evaporative water loss. Those four birds caught during the second winter, provided data of O_2 consumption, CO_2 production, and evaporative H_2O loss during measurements carried out from January, 1967, through February, 1967. A Beckman paramagnetic oxygen analyzer monitered O_2 consumption which was recorded by a Brown single strip recorder. Silica gel and ascarite were used to gravimetrically determine evaporative H_2O loss and CO_2 production, respectively. The apparatus used for the experiments (Figure 3) allowed either single or simultaneous measurement of any one of the above parameters.

A small aquarium pump provided the air flow which passed successively via rubber, copper, and glass tubing connections to, (1) a surge tank, (2) cylinders of silica gel and ascarite for removal of water vapor and CO_2 from the air, (3) a valve controlling the air flow through the metabolism chamber, (4) a metabolism chamber contained in a constant temperature cabinet, (5) a pressure gauge, (6) a second, "double", system of chemical absorbants for removal and testing of the respiratory products from the post chamber air flow, (7) a flow meter, (8) a bleeder valve for pressure regulation, (9) a gas selector panel, (10) a final dehydration cylinder, (11) a cotton filter, and (12) the Beckman oxygen analyzer.

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Flow rates in this open system were regulated from 320 cc to 628 cc of air per min (uncorrected to STP), and pressures in the metabolism chamber were maintained between 6 to 12 mm Hg, which gave an absolute pressure to the system between 670 and 690 mm Hg.

Coiling of the tubing in the constant temperature cabinet allowed the air to be cooled or warmed to the test temperature before it entered the metabolism chamber. The metabolism chamber consisted of a new one gallon paint can, the lid of which was fitted with (1) an inlet port which extended 3/4 of the way into the can to allow complete circulation of air within the chamber, (2) an outlet port, and (3) an arrangement for a thermistor probe with which to monitor the temperature within the chamber. A 1/2 in mesh hardware cloth floor, set about 7 cm from the bottom of the can on legs constructed from copper tubing, held the bird away from the bottom which was covered to a depth of about 2 cm with mineral oil. The mineral oil served to trap feces voided by the bird, thereby eliminating the possible addition of fecal and urinary water to the system. The chamber also contained a perch on which the bird could sit in a normal posture.

The freezer chest of a refregerator was converted into a controlled temperature cabinet by placing in it, a hair dryer wired to a manually controlled thermostat and variable transformer. The heating element of the hair dryer thus opposed the refrigerating unit to keep any temperature within the range from -16° C to 43° C, constant within plus or minus 0.5° C. Dry ice placed in the temperature cabinet, kept temperatures constant to plus or minus 1° C, below -16° C.

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Figure 3—Schematic diagram of the apparatus.

P . . . . . Pump
T . . . . . Surge tank
C . . . . . Coiled tubing
MC. . . . . Metabolism chamber
HD. . . . . Hair dryer
VT. . . . . Variable transformer
TH. . . . . Thermostat
TC. . . . . Temperature cabinet
PG. . . . . Pressure gauge
FM. . . . . Flow meter
SP. . . . . Gas selector panel
F . . . . . Filter
1, 2, 3, . . U tubes of silica gel
4, 5, 6, . . U tubes of ascarite
V_1. . . . . Valve controlling the flow rate
V_2. . . . . Bleeder valve
V_3. . . . . Valve regulating the 20.93 % reference gas
V_4. . . . . Valve regulating the sample air flow
V_5. . . . . Valve regulating the 12 % reference gas
$3V_1$ . . . . 3-way valve } Detours the sample flow for H_2O and CO_2
$3V_2$ . . . . 3-way valve }
$S3V_3$. . . . 3-way solenoid valve
E . . . . . Exhaust from the analyzer

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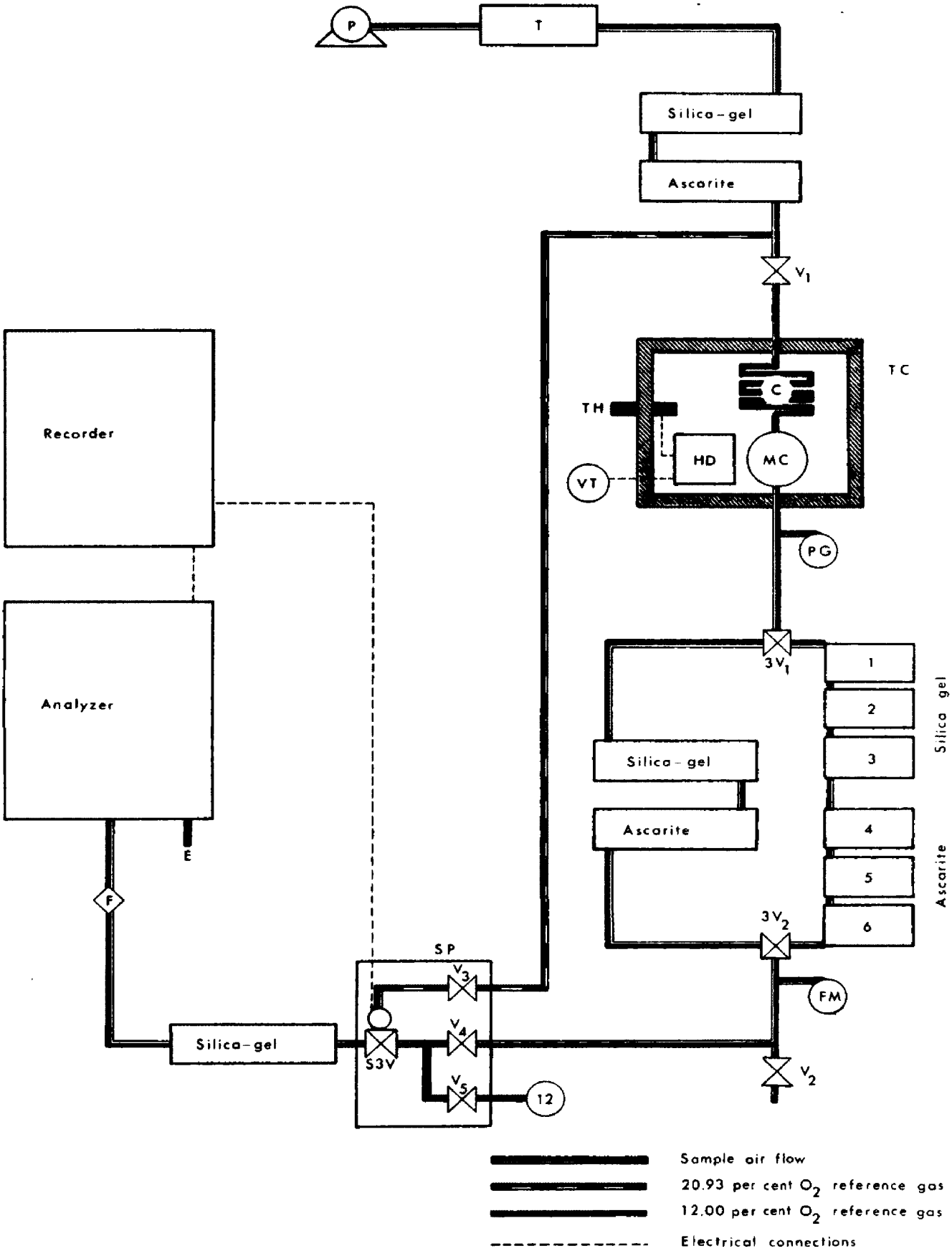

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The pressure gauge, calibrated to be read in mm of Hg, installed in the flow line near the outlet port of the animal chamber, consisted of a mannometer tube containing Brody's mannometer fluid. The flow meter, calibrated to be read in cc of air/min, installed in the flow line just downstream from the CO_2 and H_2O vapor sampling system, consisted of a glass U tube containing Bordy's mannometer fluid, which utilized the Venturi effect to indicate the volume of air (uncorrected to STP) flowing through the animal chamber.

During 20 minute intervals of some experiments, air from the outlet port was diverted to a detour line, and passed through three U tubes each, of silica gel and ascarite. These chemical absorbants were used to gravimetrically determine to the nearest milligram the evaporative H_2O loss and CO_2 production, respectively, of the bird being tested. Cylinders of like, chemical absorbants in the main flow line, dryed and removed the CO_2 from the post chamber air when O_2 consumption alone was being tested. Periodic tests using an empty metabolism chamber, indicated there were no leaks or water vapor in the apparatus.

A needle valve in the gas selector panel allowed aliquots of sample air, at 150 cc/min, to enter the analyzer. Two other needle valves in the gas selector panel regulated the flow into the analyzer of either, dry room air containing 20.93 % O_2, or a commercially mixed gas containing 12 % O_2. These were used as reference gases to set the zero point and span, respectively, of the analyzer. The analyzer could then detect the O_2 concentration of a gas mixture containing from 12 % to 20.93 % O_2. (For a more complete description see the Beckman Instruction Manual No. 81043--B, 1962). From the gas selector panel, the air from either of

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the three valves passed through a final cylinder of silica gel, and a cotton filter before entering the analyzer.

The analyzer determined the partial pressure of the O_2 in an aliqout of air flowing into it by measuring its magnetic susceptibility. Because O_2 if highly paramagnetic and the other atmospheric gases are weakly diamagnetic, the O_2 molecules placed in a magnetic field act as a temporary magnet, analogous to a piece of soft iron in a magnetic field. The other gases in the sample being diamagnetic, act as a non-magnetic particle in a magnetic field (Beckman Instruction Manual, 81043--B, 1962). The analysis cell of the analyzer constantly detects any change in the partial pressure of the O_2 in the sample. This information is transmitted electrically to the Brown single strip recorder, where it is continuously transcribed on a moving chart, not as partial pressure but as percent of O_2 present in the sample. From this recorded reduction in concentration, and the rate of flow, the rate of O_2 consumption per g body weight per hour, can be calculated using conversion factors and equation (10) of Dapocas and Hart (1957).

The corrected volume of air flowing through the animal chamber was calculated using the following conversion factor:

$$V_e = (V_1)\left(\frac{263}{(273 + T)}\right)\left(\frac{TP}{760}\right)$$

where V_e is the volume of dry gas at 0^o C and 760 mm Hg; V_1 is the original volume; T is the temperature in degrees centigrade; and TP is the barometric pressure plus the pressure in the system.

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The partial pressure of O_2 in both the inlet and outlet ports was determined according to the following equations:

$$P_{IO_2} = (\%IO_2)\ (BP)$$

$$P_{IO_2} = (\%EO_2)\ (BP)$$

where P_{IO_2} is the partial pressure of O_2 in the inlet air; P_{EO_2} is the partial pressure of O_2 in the outlet air; $\%IO_2$ is the percent of O_2 in the inlet air (20.93% constant); $\%EO_2$ is the percent of O_2 in the outlet air (from the analyzer record); and BP is the barometric pressure.

Oxygen consumption was then calculated from the Depocas and Hart (1957) equation:

$$V_o = V_e \frac{P_{IO_2} - P_{EO_2}}{BP - P_{IO_2}}$$

where V_o is the O_2 consumption per minute; V_e is the volume of dry air at 0° C and 760 mm Hg; P_{IO_2} is the partial pressure of O_2 in the inlet port; P_{EO_2} is the partial pressure of O_2 in the outlet air; and BP if the barometric pressure.

The O_2 consumption per minute was then converted to the O_2 consumed per gram body weight per hour.

All 20 minute CO_2 and H_2O vapor collections were taken only when the rate of O_2 consumption was constant and indicated the bird was at rest. Water loss measurements were extrapolated to represent an hour and plotted as milligrams of H_2O lost per gram body weight per hour. The weight of the CO_2 measured was extrapolated to represent an hour. It was then converted to a volume (Lg CO_2 = 1.977 LCO_2) and divided by the O_2 consumed during that same perios to give the respiratory quotient. The ratio of heat lost to heat produced (the e/p ratio) was calculated using 4.8 Kcal/L as the caloric equivalent of the O_2 consumed, and .58 Kcal/g as the heat of vaporization of the

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RESULTS

I. Oxygen Consumption.

Oxygen consumption increases linearly when plotted with decreasing temperature from 30° C to -15° C (Figure 4). The regression line representing this increase is expressed by the equation:

$$cc\ O_2/g \times hr^{-1} = 10.20 - .20t$$

where t is the ambient temperature. At temperatures below -15° C, values for oxygen consumption become more scattered and several points rise markedly above the linear relationship. The regression line of increasing oxygen consumption extrapolates to zero metabolism at about 51° C which is far above the range of normal body temperatures (42° C to 43° C from Wetmore, 1921).

These birds consumed the least amount of oxygen between ambient temperatures of 30° C to 39° C. The basal or resting rate of oxygen consumption calculated from data within this temperature range is 3.71 cc $O_2/g \times hr^{-1}$. At 40° C and above oxygen consumption increases with increasing temperature to values between 4.2 and 7.0 cc $O_2/g \times hr^{-1}$.

The metabolism of summer birds in response to changing temperatures does not differ from that of winter birds.

II. Evaporative Water Loss.

Evaporative water loss increases directly with increasing temperature, though not at a constant rate (Figure 5). From 0° C to 21° C water loss is relatively constant and remains below 5 mg/g x hr^{-1}. From 22° C to 39° C water loss increases gradually. Over this 17° C interval the Q_{10} is about 2.2. At 40° C and above, water loss values increase tremendously.

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Figure 4—Oxygen consumption of the red-breasted nuthatch in cc $O_2/g \times hr^{-1}$, plotted in respect to ambient temperature ($T_a{}^{o}C$). Closed circles represent summer birds and open circles winter birds.

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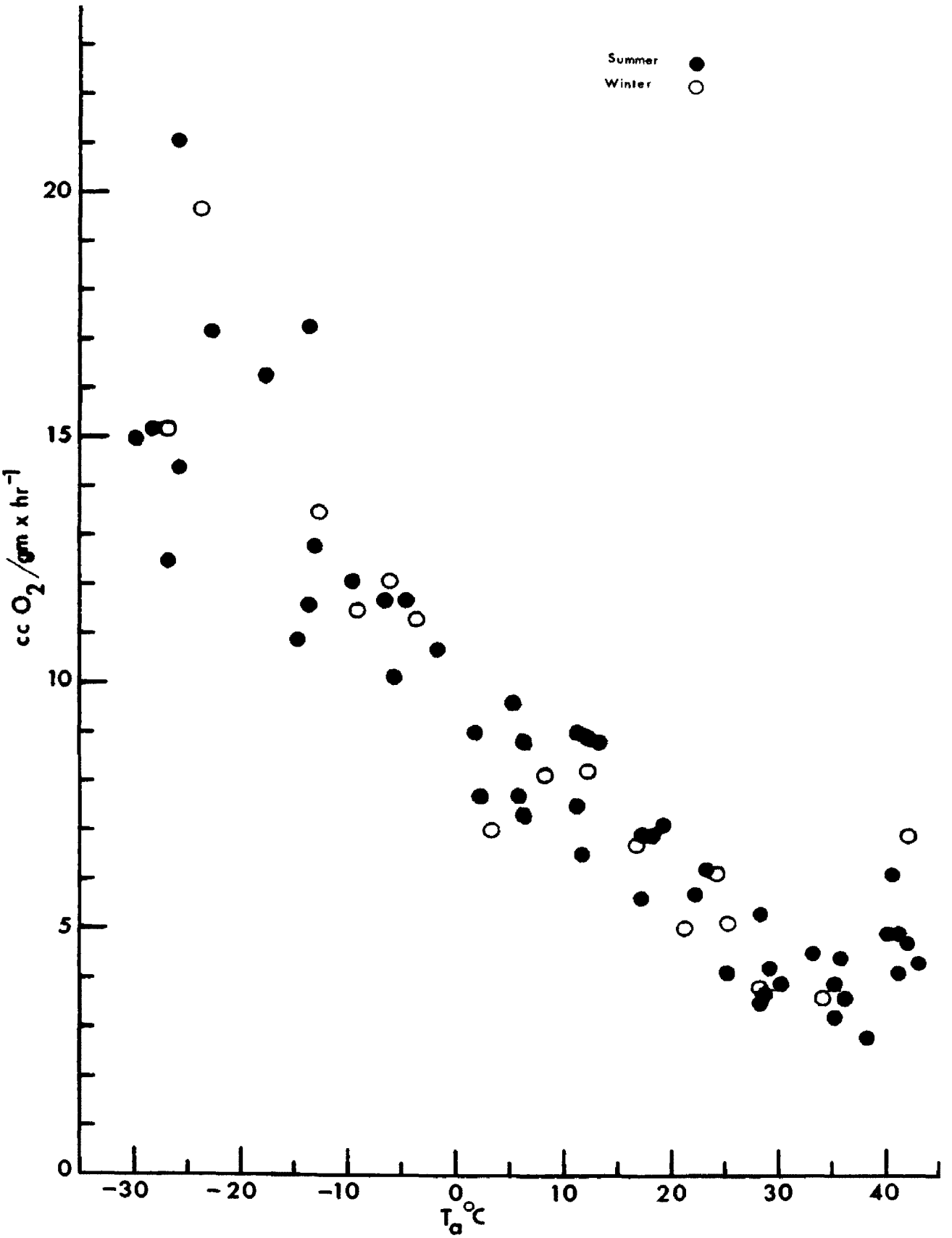

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Figure 5--Evaporative water loss of the red-breasted nuthatch in mg/g x hr^{-1}, plotted in respect to ambient temperature (T_a°C). See legend for figure 4.

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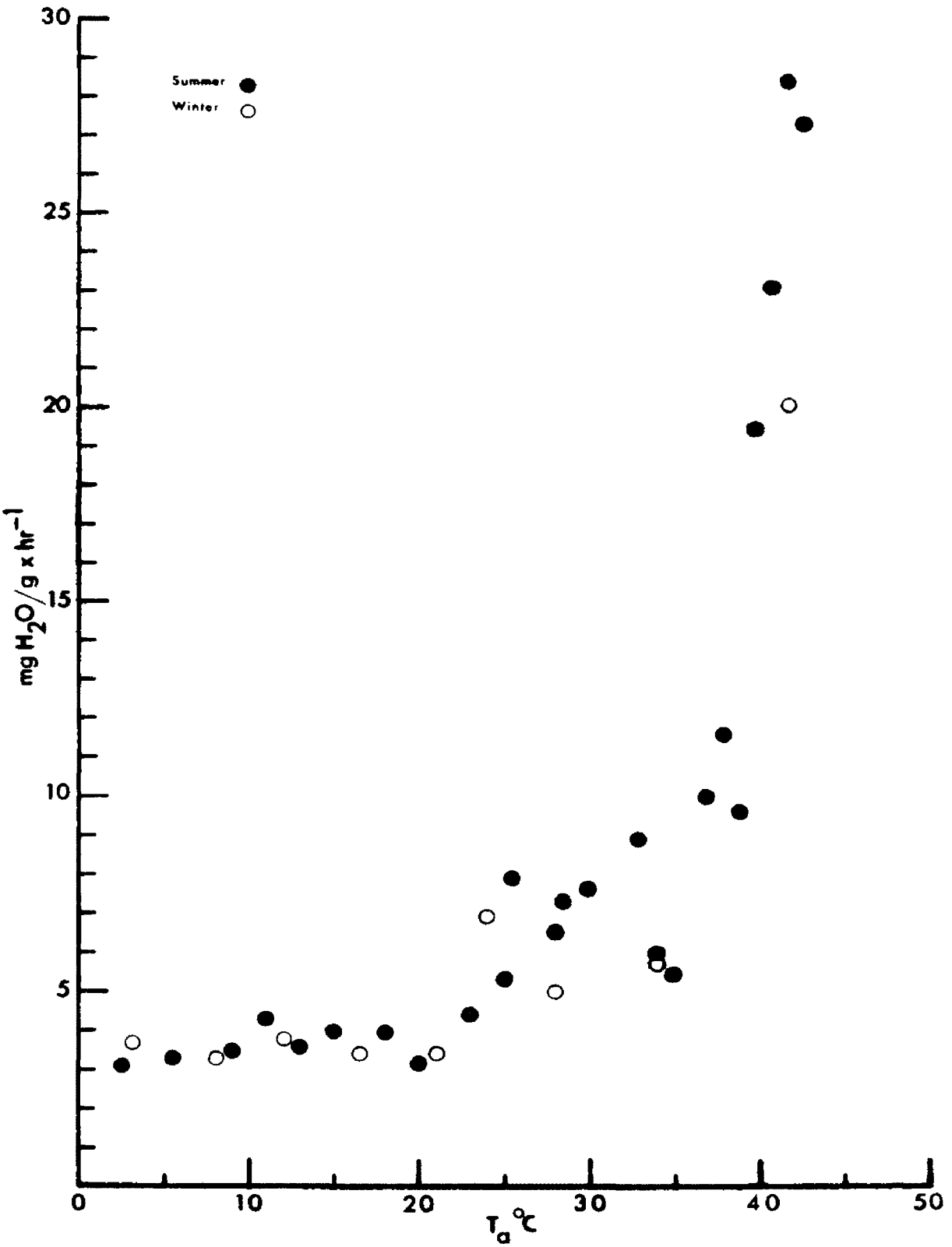

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III. The Respiratory Quotient.

Experimental respiratory quotients for the red-breasted nuthatch ranged from 0.43 to 1.3. These were plotted in relation to temperature in Figure 6. The graph shows a correlation of low respiratory quotients at low ambient temperatures and high respiratory quotients at high ambient temperatures. The summer birds (closed circles) show the greatest variation giving both the highest and lowest values at both the upper and lower ends of the temperature scale. The values for the winter birds (open circles) fit the scatter of summer values except at temperatures above 25° where they are below the scatter of summer values.

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Figure 6--Respiratory quotient (R. Q.) of the red-breasted nuthatch as plotted against temperature (T_a°C). See legend for Figure 4.

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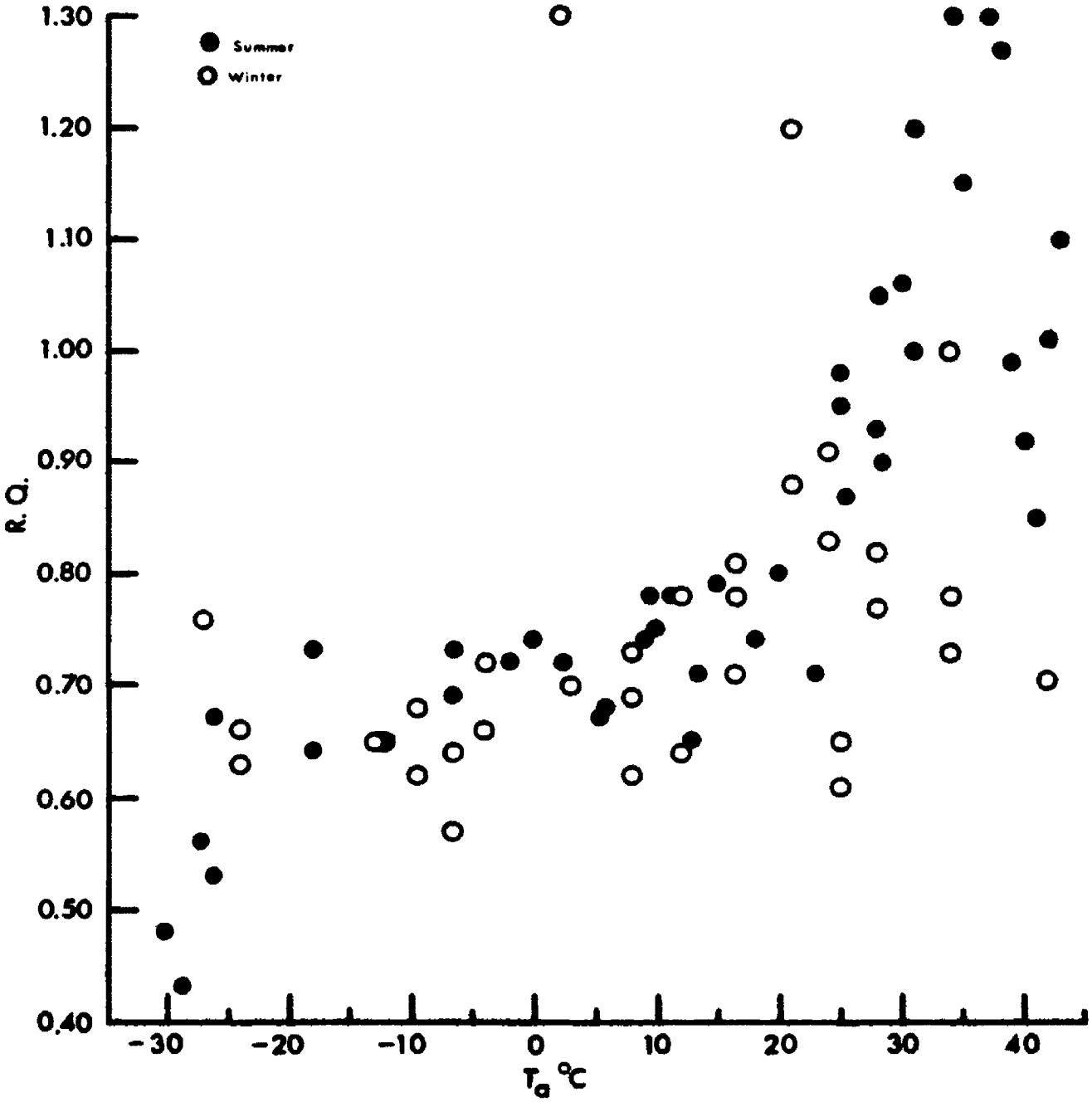

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DISCUSSION

I. The Resting (basal) Metabolic Rate.

The resting metabolic rate of the red-breasted nuthatch is compared in Table 1 with those values predicted for a bird of comparable size by the various equations available. The resting rate of the nuthatch is very similar to the value predicted by Lasiewski and Dawson (1967) for passerines, but is more than 40 % higher than those values predicted for a comparably sized bird by the Lasiewski and Dawson (1967) equation for nonpasserines, or the King and Farner (1961) equation for large birds. These comparisons agree with Lasiewski and Dawson's hypothesis that passerines have a greater metabolic rate than nonpasserines of comparable size, and that the metabolic rate-body weight curve for passerines has the same slope as that for nonpasserines, but its y intercept is higher. The metabolic rate of the red-breasted nuthatch is twice that of a comparably sized mammal.

II. Energy Requirements in the Cold.

The increase in oxygen consumption below 30° C indicates the red-breasted nuthatch must elevate its metabolic rate to equate heat gain with heat loss. The line representing this increase extrapolates to above the range of normal body temperatures, therefore, thermal conductance in this bird probably decreases regularly over a wide range of temperatures below 30° C. Such a continuing decrease in conductance may be the result of a decrease in body temperature (Bartholomew, 1964; Dawson, 1958; Dawson and Tordoff, 1959, 1964; Hart, 1957, 1962; Herreid and Kessel, 1967; King, 1964; Leitner, 1966; Misch, 1960; Scholander, 1950b; Veghte, 1964;

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TABLE I--The basal metabolic rate of the red-breasted nuthatch (3.7. cc O_2/g x hr^{-1}) and its relationship to predicted values.

EQUATION AND REFERENCES	PREDICTED VALUE IN cc O_2/g x hr^{-1}	PERCENT DIFFERENCE OF THE PREDICTED VALUE FROM THE EXPERIMENTAL VALUE
Lasiewski-Dawson (1967) Passerines	3.58	3.55
Lasiewski-Dawson (1967) Nonpasserines	2.17	41.60
Lasiewski-Dawson (1967) All birds	3.12	15.90
King-Farner (1961) Large birds	1.93	48.10
King-Farner (1961) All birds	3.00	19.20
Brody-Proctor (1932) All birds	3.60	2.97
Kleiber (1961) Mammals	1.69	54.50

Veghte and Herreid, 1965; West, 1962; West and Hart, 1967). That this nuthatch did lower its body temperature is not known, but this response has been reported regularly in the literature for other small birds (see Introduction). Because the body temperatures of these nuthatches were not measured the ambient temperature at which conductance did reach its minimal value cannot be determined. Assuming from oxygen consumption data alone, that conductance in fact did decrease over a wide range of ambient temperatures, then these birds could use this response to reduce

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the energy needed for maintaining a constant body temperature during periods of inactivity at low ambient temperatures.

Because exposure time to ambient temperatures near and below -15° C was short, some of these birds may have resisted dropping their body temperatures during these measurements. Therefore, the very high oxygen consumption values of five of these birds may have been the result of higher requirements to maintain their body temperatures.

During the day the nuthatch obviously produces heat by activity but during cold nights it apparently shivers like other birds to produce the required body heat (Hart, 1962; Steen and Enger, 1957; West, 1965). Shivering movements were observed in nuthatches on the perch of the animal chamber immediately following exposure to cold.

Several species of birds differ in their ability to increase food consumption and absorption in response to decreased photoperiod and temperature (Brenner, 1966; Cox, 1961; Davis, 1955; Kendeigh, 1949; Seibert, 1949). The nuthatch probably eats and/or absorbs more food to supply the extra energy it needs to maintain a constant body temperature during the long cold winter night than it needs during the shorter warmer nights of summer.

Moore (1945) in discussing the winter night habits of birds mentioned roosting in cavities and other sheltered areas to reduce heat loss. Kendeigh (1961) measured the possible energy conserved by a house sparrow roosting in a nest box and suggested from his results that this behavior may well be the factor allowing the northward extention of many small species. Roosting habits of the red-breasted nuthatch are undescribed but I found them utilizing the nest boxes in the outdoor flight cage on

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two occasions. In congeners, the pigmy nuthatch (Sitta pygmaea) (Knorr, 1957)and brown-headed nuthatch (Sitta pusilla) (Norris, 1958) communal roosting in cavities is common.

III. Oxygen Consumption at High Temperatures.

The increase in oxygen consumption for (Sitta canadensis) at ambient temperatures above 39° C reflects the energy expended in evaporative cooling. These birds were often observed in the summer, both during captivity and in the wild, hanging upside down with feathers tightly compressed, mouths agape, and panting.

IV. Oxygen Consumption of Summer and Winter Birds.

The values for oxygen consumption obtained from the four winter animals fit into the scatter pattern of the values obtained from the 12 summer animals so well that no differences are apparent. The small size of the winter sample may account for this, but because none of the birds tested in these experiments showed any sign of molting, they were probably also in full plumage; therefore, differences in oxygen consumption of summer and winter birds due to differences in the insulative quality of the feathers would not be expected. Further experiments determining the survival time at different photoperiods and different ambient temperatures at different seasons when ad lib food is provided, may better reveal any seasonal metabolic acclimatization which may occur in this species.

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V. Evaporative Water Loss and Dissipation of Metabolic Heat.

A. Evaporative Water Loss.

The low rate of water loss of the nuthatch at ambient temperatures below 20° C indicates that water loss is a passive process at these temperatures (Figure 5). The gradual rise in water loss between 22° C and 39° C probably reflects the ability of warmer air to carry a greater mass of water vapor, rather than it does any active efforts of these birds to lose heat at these ambient temperatures. Furthermore, the record of oxygen consumption (Figure 4) indicates these birds actively produce heat over most of this temperature range so heat loss is not a problem. The bulk of heat lost in this range of moderate temperatures is controlled via adjustments of the plumage to facilitate radiation, conduction, and convection. The efficiency of these avenues of heat loss may be further enhanced by dermovascular dilation, and/or elevation of the body temperature to increase the thermal gradient between the body and the environment (Dawson and Schmidt-Nielsen, 1964; Hudson, 1962; Hudson and Bartholomew, 1964; King and Farner, 1964).

The curve for water loss with temperature breaks sharply upward at approximately 40° C and indicates that panting must be initiated to prevent accumulation of body heat and elevation of the body temperature.

Lasiewski *et al.* (1966) demonstrated that the relative humidity in the metabolism chamber is inversly related to the rate of the flow of air through it. The relative humidity in turn affects the amount of water that can be evaporated from the respiratory surfaces (King and Farner, 1964;

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Lasiewski et al. 1966) and hence directly affects the ability of the bird to dissipate heat by this method. One preliminary experiment during this study, conducted with a relatively low flow rate of 120 cc air/min, and a ambient temperature of 41° C illustrated these principles. Moisture in the chamber, resulting from a high relative humidity soaked the birds feathers and he survived these conditions only 3 hours. Estimation of the relative humidity in the metabolism chamber used in this experiment, from the formula:

$$\% \text{ RH} = 100 \frac{x/y}{z}$$

given by Lasiewski et al. (1966) where x is the amount of H_2O vapor added in mg/min, y is the air flow rate in 1 min, z is the density of saturated stream at the temperature of the chamber, reveals it was never over 15% at the flow rate of 620 cc air/min (uncorrected to STP) used in all but the first six of these experiments. Evaporative H_2O loss was not measured in the first six experiments, and none of them were conducted at ambient temperatures exceeding 39° C. Because of the wide range of flow rates used throughout the literature, and the variations in relative humidity which result, no attempt has been made to directly relate the weight of water lost by this nuthatch to that lost by other birds. In general evaporative loss per gram body weight increases inversely with decreasing body weight in several species (Bartholomew and Dawson, 1953).

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B. Dissipation of Metabolic Heat.

Because oxygen consumption and water loss were measured simultanously in these experiments, the relative effectiveness of the bird's evaporative cooling can be estimated. This relationship is shown in Figure 8 as the e/p ratio (e = the heat lost in calories by evaporative cooling, and p = the metabolic heat produced in calories) which illustrates the percent of the metabolic heat which is lost by evaporative cooling. The results shown in these experiments indicate quite accurately the effectiveness of evaporative cooling in this species. These nuthatches increase water loss tremendously at temperatures above 37° C, and at 42° C and 43° C they dissipate 74 to 77 % of their metabolic heat by evaporative cooling (Figure 8). Birds generally appear reluctant to lose valuable water for such cooling and store heat by insulative adjustments, thereby raising body temperatures to within tolerated limits and consequently increasing passive heat loss to the environment (King and Farner, 1964). However, if environmental temperatures exceed the body temperatures tolerated by the bird then body heat can only dissipated by evaporative cooling.

Activity reduces the efficiency of evaporative cooling as is demonstrated by the e/p ratio of the winter bird at 42° C. This bird was active throughout this test, and had the highest metabolic rate of any bird tested at high ambient temperatures. Consequently its e/p ratio (Figure 8) measures slightly over 50 %. Reduction in activity and avoidance of direct insolation, therefore, could well be prerequisites for birds to prevent a lethal rise in body temperature when exposed to high ambient temperatures.

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Figure 7-- The e/p ratio for the red-breasted nuthatch plotted with ambi
temperature (T_a°C). See legend for Figure 4.

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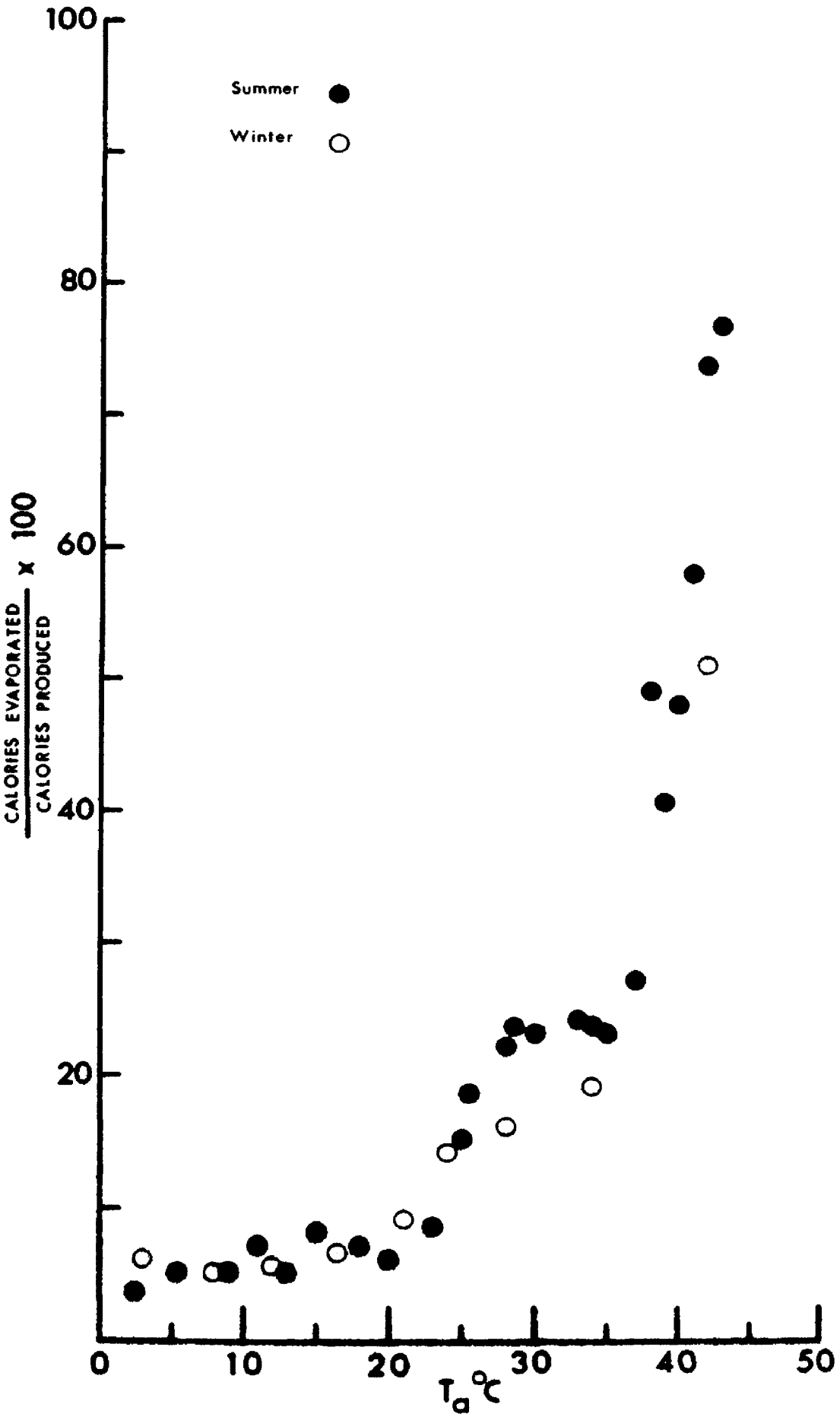

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VI. The Respiratory Quotient.

Several authors (Kendeigh, 1944; Salt, 1952; and Wallgren, 1954) have found that small passerines reach a post-absorptive state after a fast of 2 to 3 hrs, characterized by a respiratory quotient of around 0.70. Red-breasted nuthatches, exposed to ambient temperatures below 26° C always produced respiratory quotients of around 0.70 even when fasted less than two hrs. White rats when exposed to cold have respiratory quotients of around 0.70 even if they are absorptive (Page, 1957; Page and Chénier, 1953). Though respiratory quotients of this nature supposedly indicate the catabolism of fats, fats may not always be utilized perferentially or exclusively as an energy source since all foodstuffs may be used at an increased rate upon short term exposure to cold. But because fat is the major reserve energy source it may be preferentially called upon to balance caloric output when caloric intake is not possible (Masoro, 1966).

The summer nuthatches when exposed for a few hours to cold produced a respiratory quotient below 0.75 but when the ambient temperature was elevated they shifted to a respiratory quotient between 0.90 and 1.0. This shift may indicate that carbohydrates may be available as a food store even after 4 to 6 hrs of fasting in the cold. Respiratory quotients indicative of fat metabolism may be due to low temperatures affecting the metabolic processes so that large quantities of CO_2 are released from the reserves possessed by the animal (Irving et al, 1930). In one instance, the shift from a low to a high respiratory quotient did not occur when the temperature was elevated, and either this animal had reached a true post-absorptive

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state, or the elevation of the ambient temperature was not enough to produce the shift.

On long-term exposure to cold in mammals, nonshivering thermeogenesis replaces the shivering thermeogenesis of short-term exposure (Hemingway, 1963) but it has not been determined what particular foodstuffs if any were used to preferentially support nonshivering thermeogensis (Masoro, 1966). Steen and Enger (1957), Hart (1962), and West (1965), indicate that nonshivering thermeogenesis does not play a role in heat production in birds even after long-term exposure to cold; therefore, cold-acclimatized birds cannot appropriately be compared with cold-acclimatized mammals because of these differences in mechanisms of heat production.

In the winter group, when the temperature of the metabolism was elevated, only one nuthatch shifted from a respiratory quotient below 0.75 to one between 0.90 and 1.0, and two birds maintained respiratory quotients between 0.76 and 0.89. Acclimatization to cold in the winter animals may allow them to use all foodstuffs, not just fat, as the calorigenic agent when they are exposed to low temperatures. Consequently carbohydrates as well as fats could be utilized at low ambient temperatures, and the depleted carbohydrate stores would allow a low respiratory quotient to occur when the ambient temperature was elevated.

The respiratory quotient of one of the winter birds taken after 2.5 hrs of fasting at 3° C was above 1.0 indicating that fat synthesis was occurring. The occurence of a respiratory quotient of this nature is not consistent with the other data obtained during these experiments. It may result from experimental error, or from the release of CO_2 from the animal's reserves (Irving et al. 1930).

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A test was conducted at an ambient temperature of 31° C with a summer animal to determine when a post-absorptive respiratory quotient could be obtained. During the third and fourth hours, the respiratory quotient was above 1.0 and after 5 hrs it was between 0.90 and 1.0. A similar experiment conducted on a winter bird at 34° C revealed respiratory quotients below 0.75 at the end of the 2nd hr, between 0.76 and 0.89 at the start of the 4th hr, above 1.0 at the start of the 5th hr, and between 0.90 and 1.0 at the end of the 6th hr. Why these birds fail to arrive at or maintain a post-absorptive respiratory quotient during periods of extended fasting at high ambient temperatures is unclear.

At ambient temperatures above 28° C for the summer birds, respiratory quotients above 1.0 often occured. The occurence of these high respiratory quotients in the winter data are less common, though this may be the result of the small number of animals for which winter data are available. If these respiratory quotients are a true indication of fat synthesis, their regular occurrence may indicate a heightened ability during the summer to produce energy-rich fat stores.

Respiratory quotient values below 0.65 were repetitive indicating that they were not artifacts of technique (Table 2). Those values below 0.60, except for one at -6.5° C in the winter group, all occur at ambinet temperatures below -15° C. These low respiratory quotients may reflect the tremendous metabolic demands made upon these birds when moved from room temperature to these extremely low ambient temperatures.

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Table 2--A summary of the respiratory quotient values below 0.65.

SEASON	TEMPERATURE °C	RESPIRATORY QUOTIENT
Summer	-30.0°	0.48
"	-28.5°	0.43
"	-27.0°	0.56
"	-26.0°	0.53
"	-18.6°	0.64
Winter	- 6.5°	0.57
"	25.0°	0.61
"	-24.0°	0.63
"	12.0°	0.64
"	8.0°	0.62
"	- 9.5°	0.62

The great variation in respiratory quotients throughout these experments illustrates that short-term respiratory quotients alone are not valid expressions of intermediary metabolism (Kleiber, 1961; Masoro, 1966). They may indicate that an animal is post-absorptive at ambient temperatures which allow expression of a resting metabolic rate, but when metabolic increases are demanded, the respiratory quotient may be distorted by any one of the reasons given in the Introduction of this paper. The wide variation of respiratory quotients for this species indicates that the intermediary metabolism of it and other small birds which are resident in climates requiring regulation of the body temperature over a wide range of ambient temperatures should be investigated via more sophisticated methods.

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SUMMARY AND CONCLUSIONS

The red-breasted nuthatch is a resident of the north temperate forests of North America. Oxygen consumption, evaporative water loss, and respiratory quotients were measured in this small species (9 to 14.2 g) to find its seasonal thermogenic abilities over a temperature range of 73° C.

In both summer and winter birds, oxygen consumption increased with decreasing ambient temperatures below 30° C at a constant rate of .20 cc O_2/°C. Between 30° C and 39° C the average metabolic rate of 3.71 cc O_2/g x hr^{-1} agrees with the predicted value for passerines.

The rate of evaporative water loss increased with increasing ambient temperature from less than 5 mg/g x hr^{-1} at 2.5° C to about 28 mg/g x hr^{-1} at 43° C. This rate of water loss indicates these birds are capable of regulating their body temperatures, in part, via this method when other avenues of heat loss become restricted or unfeasible. The red-breasted nuthatch is capable of dissipating more than 70 % of its metabolic heat through evaporative cooling at very high ambient temperatures.

Respiratory quotients ranged from 0.43 to 1.3 over the 73° C temperature range studied. They indicate that a change in catabolism occurs between low ambient temperatures and high ambient temperatures. A shift of respiratory quotient with a rise in ambient temperature is also described. This shift, and other variations in the respiratory quotient are discussed.

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